University of Alberta

Genetic Analysis of Seasonal Seedling Height Growth Curves and Early Selection in White Spruce

by

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ABSTRACT

Genetic analysis was conducted on parameters of the logistic growth curve for seasonal height growth, absolute height and height increments, stem tissue components, root collar diameter, fresh and dry weights, seedling architectural traits, dated for budburst, and branch and needle characteristics of white spruce seedlings grown in the greenhouse at the University of Alberta, Canada. The objective was to identify which of these juvenile traits best predict 10 and 11-year field height at Chinchaga (site A) and Saddle Hills (site B), Alberta. The 58 open-pollinated families tested were selected for their superior phenotype from the Peace River area Alberta.

Because of very low heritability for height at site B, only the results with site A provide better estimates of selection efficiencies, the measure used to judge the feasibility of early selection in this study. At age 11 years on site A (AH11), the selection efficiency for first season height (FH2-FH18) was 41.5-55.5% and that of the second season height increment (SH2-SH18) and 36-week height (TH36) was -8.9-7.7% and 8.4%, respectively. The rate of growth (r) and age at the point of inflection ($t_{0.5}$) of the growth curve had respectively, selection efficiencies of -6.2% and 22.3% (first season) and 17.2% and -26.2% (second season). Thus, first season height was a better predictor of field height than the second season height, and seasonal height growth curve parameters.

Branch length (BL), the number of stem units (NSU) and stem unit length (MSUL) had selection efficiencies of 17.6%, 3.2% and 33.6%, respectively. Terminal (TB2) and branch (BB2) budburst, and needle length (NL) had selection efficiencies of 15.3% and 13.9%, and 17.6%, respectively. Considering the short time involved in greenhouse testing, selection for FH2-FH18 and MSUL would be efficient in improving

field height growth at site A for the tested families. Selection indices combining AH11 and two greenhouse traits would increase genetic gain of field height by 1-8% compared with selection for AH11 alone. This shows that apart from identifying juvenile traits that are good indicators of field height, retrospective studies can provide additional information to enhance selection efficiency of field height.

TO MY DAUGHTERS

Lucia Kemilembe **and** *Jasinta Kengonzi*

AND MY SON

Francis Rutatiina

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TABLE OF CONTENTS

CHAPTER I: **INTRODUCTION AND LITERATURE REVIEW**

1.1.Introduction.....1

1.2. Literature Review.....7

1.2.1. The Species and its Ecology.....7

1.2.2. Reproductive Biology.....8

1.2.3. Genetic Variation in White Spruce.....11

1.2.3.1. Variation in Growth Potential.....12

1.2.3.2. Variation in Wood Properties.....14

1.2.3.3. Variation in Phenology.....15

1.2.3.4. Biochemical and Molecular Variation.....18

1.2.4. Review on Early Selection.....18

CHAPTER II: **MATERIAL AND METHODS**

2.1. Description of the Test Material.....30

2.2. Experimental Procedures.....30

2.2.1. Field Trials and Assessment.....30

2.2.2. The Greenhouse Retrospective Study.....31

2.3. Data Analysis.....38

2.3.1. Modelling of Stem Height Growth.....38

2.3.1.1. First and Second Season Growth Curves.....38

2.3.1.2. Choice of Growth Model.....39

2.3.1.3. The Simple Logistic Model.....44

2.3.2. Genetic Analysis.....51

2.3.2.1. General Analysis of Greenhouse Data.....51

2.3.2.2. Analysis of Tissue Components.....53

2.3.2.3. Analysis of Field Data.....57

2.3.2.4. Efficiency of Early Selection.....59

2.3.2.5. Symbols and Definitions of Traits.....64

CHAPTER III: **RESULTS**

3.1. Introductory Remarks.....68

3.2. Results from the Greenhouse Study.....68

3.2.1. Height and Growth Curves.....68

3.2.1.1 Variances and Heritability.....68

3.2.1.2. Correlation Coefficients.....75

3.2.2. Root Collar Diameter.....88

3.2.3. Budburst, Branch and Needle Characteristics.....90

3.2.4. Biomass Production.....92

3.2.5. Tissue Components.....96

3.2.6. Seedling Architecture.....100

3.3. Results from Field Trials.....103

3.4. Efficiency of Early Indirect Selection.....105

3.4.1. Heritability for Reduced Datasets.....105

3.4.2. Greenhouse-field Genetic Correlations.....105

3.4.3. Correlated Genetic Gains.....115

3.4.4. Efficiency from Early Selection.....120

3.5. Multiple Trait Gain Efficiencies.....126

3.6. Genotype-Environment Interaction.....129

CHAPTER IV: **DISCUSSION AND RECOMMENDATIONS**

4.1. Genetic Implications for Height and Height Growth Curves.....130

4.1.1. Greenhouse and Field Height Growth.....130

4.1.2. Growth Curve Parameters.....133

4.2. Genetic Implications for Other Traits.....141

4.2.1. Root Collar Diameter.....141

4.2.2. Biomass Partitioning and Seedling Architecture.....142

4.2.3. Dates for Budburst.....148

4.2.4. Branch and Needle Lengths.....149

4.2.5. Tissue Components.....150

4.3. Feasibility of Early Selection.....154

4.4. General Conclusions.....172

4.5. Recommendations.....174

LITERATURE CITED.....177

APPENDICES.....186

LIST OF TABLES

Table 1: Goodness of fit for the different growth models evaluated for fitting height growth curves. 42

Table 2: Analysis of variance and covariance for the greenhouse data....52

Table 3: Analysis of variance and covariance for tissue components....54

Table 4: Analysis of variance for field height....57

Table 5: Ranking of families for field and greenhouse height....64

Table 6: Variance components and heritability for greenhouse first season height growth....69

Table 7: Variance components and heritability for greenhouse second season height growth....70

Table 8: Range of family means for growth curve parameters....71

Table 9: Variance components and heritability for growth curve parameters....72

Table 10: Variance components and heritability for cumulative height....74

Table 11: Correlation coefficients for cumulative height....79

Table 12: Correlation coefficients for first season height and growth curve parameters....80

Table 13: Correlation coefficients for second season height and growth curve parameters....83

Table 14: Correlation coefficients between growth curve parameters....86

Table 15: Correlation coefficients between seasonal growth curve parameters and cumulative height....87

Table 16: Variance components and heritability for root collar diameter....88

Table 17: Correlation coefficients between cumulative height and root collar diameter....89

Table 18: Correlation coefficients between root collar diameter and seasonal height growth curve parameters....90

Table 19: Variance components and heritability for branch, needle and phenological traits....91

Table 20: Correlation coefficients for budburst with height and root-collar Diameter....92

Table 21: Variance components and heritability for fresh and dry weight....93

Table 22: Correlation coefficents for fresh and dry weight traits....94

Table 23: Pearson's correlation coefficients between dry weights and growth-related traits....95

Table 24: Variance components and heritability for tissue components....96

Table 25: Correlation coefficients between tissue components....97

Table 26: Relative degrees of determination of height by tissue components....98

Table 27: Correlation coefficients between tissue components and stem height....99

Table 28: Variance components for seedling architecture traits....100

Table 29: Pearson's correlation coefficients between seedling architecture traits and growth-related traits....102

Table 30: Variance components, heritability and genetic gains for field height....104

Table 31: Genetic correlation coefficients between greenhouse traits and field height when all 58 families are included....106

Table 32: Genetic correlation coefficients between greenhouse traits and field height when 15 families with extreme rank change are excluded....112

Table 33: Correlated genetic gains in field height as the result of selection on juvenile greenhouse traits....116

Table 34: Gain efficiencies from early selection on juvenile greenhouse traits for improving field height....122

Table 35: Gain efficiencies for multiple trait selection for site A....128

Table 36: Correlation coefficients between the two field test sites....129

Table 37: Examples of heritability values for parameters of the weight-age growth curves in domestic animals....135

LIST OF FIGURES

Figure 1: Scatter plot and the regression of the residues on predicted height for the for the first season data.....46

Figure 2: Scatter plot and the regression of the residues on time for the first season data.....46

Figure 3: Scatter plot and the regression of the residues on predicted height for the for the second season.....47

Figure 4: Scatter plot and the regression of the residues on time for the first season data.....47

Figure 5: Scatter plot and the regression of predicted height on observed height for the first season data.....48

Figure 6: Scatter plot and the regression of predicted height on observed height for the second season data.....48

Figure 7: Scatter plot and the regression of residues on predicted height for the first season data based on the method of selected points.....49

Figure 8: Scatter plot and the regression of predicted height on observed height for the first season data based on the method of selected points.....49

Figure 9: Scatter plot and the regression of residues on predicted height for the Second season data based on the method of selected points.....50

Figure 10: Scatter plot and the regression of predicted height on observed height for the second season data based on the method of selected points.....50

CHAPTER I: INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

White spruce (*Picea glauca* (Moench) Voss) is an important pulp and timber tree species in Canada and the Lake states of the USA. Its high genetic variability and commercial importance make it an interesting species for genetic studies and tree improvement (Stiel 1976). Because of its slow growth (Hosie 1969; Scoggan 1978), selection for genetic improvement of white spruce has to be done at young ages. However, selection at young ages is meaningful only if superior growth of young genotypes reflects superior growth of mature genotypes (Namkoong et al. 1988). Therefore, identification of high-ranking genotypes for growth using juvenile traits that are persistent throughout the rotation period is a key to successful improvement of a mature trait.

One of the main objectives of tree breeding is to increase wood production (volume per hectare). However, volume production is governed by its component traits namely height, diameter and stem taper. Of these three traits, height growth is the most assessed one in tree seedling experiments (Danjon 1994), since it is easily measured (Kremer 1992) and the fact that height might be the only yield-related trait that is well expressed in tree seedlings. Therefore, tree breeders working to improve volume production by selecting genotypes at a seedling stage have to rely mainly on juvenile height growth as a selection criterion for mature volume production.

In forest trees, selection to improve height at rotation age is often based on absolute height that has accumulated for a specified number of years (growing seasons). However, total height is the sum of annual height increments and will, therefore, be better predicted through genetic analysis of its composite annual increments rather than

cumulative height at a specified age (Kremer 1992). In addition to selection based on annual increments, it is suggested that selection based on the pattern of growth (growth curve) might be a better way of improving mature height than selection based on absolute height at a given age (Magnussen and Kremer 1993). Study of growth curves reveals how genotypes achieve their annual height growth. Thus, selection on height growth curves is often more related to the breeder's objective, i.e., manipulation of height growth to achieve maximum gain than selection on absolute height. Consequently, growth can be better maintained by selection on parameters of the growth curve such as the rate of growth than selection on absolute height (Magnussen and Kremer 1993). Another advantage of growth curve analysis is that a long series of periodic measurements of the same trait provide information that is difficult to interpret. Growth curve analysis reduces these measurements into a few biologically interpretable variables that explain growth-age relationship much better than raw data of periodic growth measurements (Brown et al. 1976; Lopez de Torre and Rankin 1978; DeNise and Brinks 1985).

Considering the pattern of growth, one question comes to mind. Is growth as depicted by total measured height at the end of the growing season influenced by the rate of growth, duration of growth, or both the rate and duration of growth? This question is of particular importance in temperate species where timing of initiation and cessation of shoot elongation is critical to the survival of young shoots from damage caused by late spring frost and early fall frost. More often, variation in frost resistance is related to variation in timing of cessation of growth as has been observed in species such as *Pseudotsuga menziesii* (Mirb) Franco (Wright et al. 1971; Rehfeldt 1983a), *Pinus contorta* Doug. (Rehfeldt 1988; Rehfeldt 1983b), and *Pinus sylvestris* L. (Wright and

Bull 1963; Mikola 1982; Kotov 1989). Genotypes that achieve much of their annual growth early in the growing season and cease to grow earlier, escape damage from fall frosts better than those that grow slowly, and thus extend growth later into the growing season. Growth curve analysis provides information on how early in a particular growing season did families of interest achieve their annual growth. Knowing this is important in breeding for frost damage avoidance.

By fitting the growth curve of seasonal height growth, we would categorise genotypes based on their rate and duration of growth. This would in turn enable us to select for tree breeding only those families with favourable combinations of the rate and duration of growth. Growth curve variables representing the rate and duration of growth for juvenile height can also be correlated with advanced-age field-height as part of the exploration for traits that are the best indicators for early selection.

Seedlings in controlled and partially controlled environments (growth chambers and greenhouses) are the most convenient materials for measuring and analysing the amount and nature of early height growth in forest trees. In controlled environments, many measurements of cumulative height growth can be made at short fixed intervals. Greenhouses and growth chambers are designed to provide favourable growth conditions during the growth period of predetermined length. In such environments, growth of seedlings is less interrupted by daily weather fluctuations than tree growth in the field. Thus, it is possible to detect height growth even at short time intervals, for example one week. In field experiments, tree growth in such a short period of time might, probably, be undetectable.

Other advantages of greenhouse and growth chamber experiments are the small size of experiments, small size of plants, and the convenient working environment. The small size of the experiment and convenient working environment allows assessment of many more traits than can be assessed in field experiments. The small size of trees (seedlings) allows assessment of traits such as biomass allocation to different parts of the plant that may be difficult to assess (especially root excavation) or assessed with large errors in large field trees. Also, traits such as number of stem units (NSU) and mean stem unit length (MSUL) that are component traits of height growth in conifers can be assessed better in the greenhouse and growth chamber than in the field.

This thesis presents the results from a study of the feasibility of early selection in white spruce from the Peace River region of northwestern Alberta, Canada. The study was a retrospective greenhouse experiment designed to assess as many juvenile traits as possible and correlate them with 10- and 11-year height at two field test locations in the province. Unique to this study is a detailed analysis of juvenile height. In this study, height was analysed in absolute terms, seasonal height increments, seasonal height growth curves, and tissue components (NSU and MSUL) using first order branch samples. Also included in the study is the destructive sampling of greenhouse seedlings to study allocation of photosynthates into branches, main stem and roots. A number of dry weights and ratios from dry weights such as harvest index (HI) and root-shoot ratio (RSR) are also included in the thesis. Other traits involved in the study include root collar diameter, branch and needle length, number of buds and branches, and the dates for terminal and branch budburst. A number of seedling architecture traits were also derived from the original traits to enable the study of the relative size of seedling parts or organs

that may have an implication on adaptation, volume production, and stability of trees against wind-throw.

The genetics of individual traits was studied in terms of genetic variances, heritability and genetic, phenotypic and environmental correlations with other traits. Finally, genetic correlations for all greenhouse traits with field-height were computed to determine the efficiency of mass selection in field-height at age 10 and 11 years as the result of indirect selection on greenhouse traits.

The thesis is organised in such a way that all chapters discuss the retrospective greenhouse study first, followed by the field tests, before the two phases of the study are brought together to discuss early selection. A brief introduction appears at the beginning of some chapters or sections outlining the contents and the scope of the chapter or section. Results are presented in such a way that similar traits appear in the same section, and each of these sections presents all genetic parameters (variances, heritability, correlations), except in cases where correlations between disimilar traits are sought.

Objectives, Study Questions and Hypothesis

Although the objectives of the study might already be clear to readers, it is necessary to state the guiding principles of this research as follows:

(a). The objectives of this retrospective study can be stated as follows:

1. To find juvenile traits in the greenhouse, which may yield high efficiencies of early indirect selection with the 10- and 11-year height in the field. This was an overall objective of the study. It underlies every trait assessed in the greenhouse.

2. To analyse growth curves for seasonal height growth as an alternative way of studying genetic variation in height growth. This objective seeks to explain genetic variation in how seasonal height increment is achieved as opposed to simply studying genetic variation in absolute seasonal height increment. Analyses of growth curves for tree seedlings are very rare in forest tree breeding. Thus, much work needs to be done in this area.

3. To determine the relative contribution of the number of stem units (NSU) and mean stem unit length (MSUL) to the fixed seasonal or annual height increment. This phenomenon is well studied in *Pinus* spp but very few studies have been done in *Picea* spp such as white spruce.

(b). The guiding study questions accompanying the above objectives are as follows:

1. What are the best early selection indicators for advanced-age height in white spruce from the Peace River region?

2. To what extent do the rate of growth and duration of growth determines seasonal height growth in white spruce seedlings from the Peace River region?

3. To what extent do the number of stem units (NSU) and mean stem unit length (MSUL) jointly determine the seasonal height increment during fixed growth in white spruce from the Peace River region?

(c). To be useful in plant and animal breeding, a trait has to have a sufficient additive genetic variance, otherwise it will not respond to selection. Therefore, all traits assessed were tested for the following hypotheses:

H_0: There is no additive genetic variance ($\sigma_f^2 = 0$)

H_1: There is additive genetic variance ($\sigma_f^2 > 0$)

where, H_0 and H_1 are the null and alternative hypotheses, respectively. σ_f^2 is the between-family (additive genetic) variance. These hypotheses apply to white spruce populations from the Peace River region, Alberta, where the tested families were sampled.

1.2 Literature Review

1.2.1 The Species and its Ecology

White spruce is a medium-sized tree that reaches the height of 25m and up to 1.0m in diameter. It has a thin scaly bark, slender branches, and a shallow root system (Den Ouden and Boom 1965; Hosie 1969). Its wood is light, soft, resilient, straight-grained and white, with little contrast between sapwood and heartwood (Hosie 1969). The main uses of white spruce are pulp and lumber production (Hosie 1969; Stiell 1976).

Ecologically, white spruce is characteristic of the boreal forest region of North America (Hosie 1969; Scoggan 1978). It is found almost everywhere in the forested regions of Canada, except the Pacific coast and the hardwood zone of southern Ontario (Stiell 1969). The natural range of white spruce extends from northern Alaska to Labrador north to latitude 58°13'(Scoggan 1978) and southward to the Atlantic coast of Maine, northern New Hampshire, Vermont, New York, Michigan, Wisconsin, Dakota and Minnesota (Den Ouden and Boon 1965; Stiell 1969; Scoggan 1978). Isolated occurrences of white spruce have also been reported in south Montana, South Dakota and Wyoming (Scoggan 1978). A more northern occurrence of white spruce at latitude 64°44' has also been reported (Sargent 1926). White spruce occurs on a variety of soils and

climates though good trees are found on well-drained moist silt soils (Hosie 1969). White spruce is mainly found in mixture with other conifers and hardwoods species, except in rare cases and mainly on disturbed sites where it exists in pure stands (Hosie 1969).

1.2.2 Reproductive Biology

White spruce is a monoecious species with male and female strobili growing separately on the same tree. Male strobili are mainly found in the middle and lower portion of the tree canopy, whereas female ones occur abundantly in the upper portion. This separation of sexual structures helps to minimise self-fertilisation, since the species is self-compatible (Wright 1964). Flowering takes place in May and seeds mature in August and September of the same year. Seed dispersal period extends from August to November (Anonymous 1948). White spruce exhibits periodicity in seed production in which heavy seed crops occur, every 2 to 6 years and light seed crops in the intervening years (Anonymous 1948).

White spruce is predominantly an out-crossing species with an average out-crossing rate of 0.9 (King et al. 1984; Cheliak et al. 1985). However, the out-crossing rate may vary among gene loci being considered, e.g., 0.75 to 0.99 (King et al. 1984). Monoecy, different locations for female and male strobili combined with wind pollination help to increase the frequency of cross-pollination and fertilisation, but do not prevent selfing. White spruce lacks genetic barriers to prevent self-fertilisation. However, it has physiological self-incompatibility mechanisms, which cause embryo breakdown following a successful self-fertilisation (Mergen et al. 1965) leading to production of

empty seeds (Mergen et al. 1965; Coles and Fowler 1976; Fowler and Park 1983; Park et al. 1984).

Even with embryo breakdown, a considerable number of self-fertilised embryos do grow to produce viable seeds. This implies that self-incompatibility in white spruce is only partial (Mergen et al. 1965). In addition, inbreeding has no effects on cone size (Mergen et al. 1965) that could otherwise affect the amount of inbred seeds produced. Studies have also shown that inbreeding depression in white spruce does not manifest itself in traits such as seed germination and early seedling growth. Viable out-crossed and inbred seeds have similar rates of germination and produce equally vigorous seedlings at least in the first few weeks after germination (Fowler and Park 1983; Park et al. 1984). Inbreeding depression does occur in such traits as advanced-age seedling survival and height growth (Mergen et al. 1965; Fowler and Park 1983; Park et al 1984).

In its undisturbed natural environments, white spruce occurs mainly in mixed stands with other conifers and hardwoods. Severe competition in these mixtures reduces the proportion of inbred saplings in the white spruce population. In most cases, seedling growth in controlled environment (greenhouse and growth chambers) takes place without competition or stresses related to drought, frost, nutrients and light inadequacies. Such ideal growth conditions mask inbreeding depression leading to normal survival and growth of inbred seedlings (Cheliak et al. 1985). Unless inbreeding is suspected, quantitative genetic analysis assumes that open-pollinated seeds, especially in wind-pollinated forest trees, are half-sib families. In this case, the between-family variance component estimates ¼ of the additive genetic variance (Falconer 1981). When the species tolerates inbreeding, this assumption is invalid, since open-pollinated seeds are

mixtures of half-sib families from cross-pollination and full-sib families from both self-pollination and pollination among genetically related trees. To prevent overestimation of heritability when inbreeding is known to exist, Cheliak et al. (1985) suggested that 3.7 rather than 4 should be multiplied with the inter-class correlation in white spruce. King et al. (1984) predicted that the proportion of half- and full sib families in open-pollinated seeds of white spruce vary among years. They suggested that progeny tests be conducted with mixture of seeds from different years. Whichever the case, adjustments should be made to avoid overestimation of the genetic variance and heritability when dealing with white spruce seedling experiments.

The longest dispersal distance for white spruce seeds was estimated at 100 metres or less, though it is believed that wind may disperse seed to a much longer distance (Rowe 1955). Coles and Fowler (1976), found that controlled crosses between trees separated by 100 metres or less produced 28% more empty seeds than crosses between trees separated by more than 100 metres. This suggests that a family structure and inbreeding exist in natural populations of white spruce. Coles and Fowler (1976) also found that related mating in natural stands of white spruce was higher in mixed than in pure stands. Undoubtedly, this is due to the effective population size being smaller in mixed than in pure stands. Therefore, when sampling trees for genetic testing or assembling a breeding population caution should be taken to avoid sampling of closely related individuals. This should include allowing sufficient distance between sample trees depending on whether the stand is pure or mixed.

White spruce hybridises freely with Engelmann spruce (*Picea engelmannii*) and Sitka spruce (*Picea sitchensis* (Bong.) Carr). This takes place in western Canada where

the natural ranges of these species overlap (Roche 1969; Stiell 1976). Some studies show that there is more infiltration (introgression) of Engelmann spruce genes into the white spruce genome than the other way round (Daubenmire 1974). In the interior of British Columbia, it is difficult to differentiate between pure trees of white spruce, Engelmann spruce, the hybrids, and other supposed varieties of white spruce because of their morphological similarities. Hence, to avoid complications in the identification of species during seed collection for reforestation purposes, the various morphological forms in the interior of British Columbia are treated as one complex, botanically, in what is known as interior spruce (Stiell 1976). Artificial hybridisation between white spruce and black spruce (*Picea mariana* (Mill.) B.S.P). has been attempted, but showed doubtful success (Wright 1955).

1.2.3 Genetic Variation in White Spruce

The natural range of white spruce is very wide in terms of latitude, longitude, and elevation. Unless climatic and edaphic factors are uniform across this vast land, white spruce should show high genetic variability in many of the quantitative traits that are subjected to natural selection. Many studies at the provenance and progeny level have been conducted in different regions of Canada and the United States of America. However, most of these studies have been localised to reflect the breeding interest of a particular region, province or state, and have thus sampled restricted parts of the species natural range. This section reviews some of the results of these studies for the most common traits.

1.2.3.1 Variation in Growth Potential

White spruce has shown high genetic variation in growth traits such as height, diameter, and traits that are derived from height and diameter such as volume and biomass production. A number of studies have shown that provenances with high growth potential come from eastern and southeastern Ontario. For example, in the Ontario study involving 91 populations collected from Ontario, Quebec, New Brunswick, Minnesota, Michigan, Wisconsin and the state of New York, Teich et al. (1975) found that the best provenances in height growth were from eastern and southeastern Ontario. Provenances from eastern and southeastern Ontario ranked high for height on southern Ontario test sites, whereas those from Ottawa Valley ranked high on northern Ontario planting sites. The genetic superiority of white spruce populations from southeastern Ontario for growth-related traits was also revealed in other provenance trials such as the one involving 22 populations from Ontario and Quebec tested in Minnesota (Stellrecht et al. 1974); 63 populations from Quebec and southeastern Ontario tested in Quebec (Li et al. 1977), and 37 populations from Ontario and Maine tested in Maine (Tebbetts 1981).

In addition to locating good seed sources for commercial tree planting, provenance trials are meant to uncover geographic trends that might guide provenance transfer. They also help us to determine environmental evolutionary pressures that might explain the current genetic structure of the species. Khalil (1986) reported on a range-wide provenance study that was conducted in the greenhouse in Ontario with 110 populations. These populations were sampled across white spruce's natural range, but the majority of these seed sources were from central and eastern Canada, and the Lake States. Far fewer populations were from western Canada and Alaska. The 4-month seedling

height growth was negatively correlated with latitude and longitude of seed origin. No relationship was found between height and elevation of seed origin. This suggests the existence of a cline in which height growth potential decreases from east to west and from south to north. In Newfoundland, a study involving 31 populations from Ontario, Quebec, New Brunswick, Wisconsin, and Minnesota showed that both the 25-year height and diameter were moderately related to longitude of seed origin ($r = -0.40$) (Hall 1986). This also points to the east-west cline with height and diameter growth potential decreasing from east to west.

In another study, 91 open-pollinated families from natural stands in the Lake States and Ottawa valley were planted in the Lake states and Petawawa, Ontario (Nienstaedt and Riemenschneider 1985). Assessments at the ages of 9 and 15 years showed that trees from the mildest climates of the south and east produced the most vigorous progeny. On the contrary, trees from the coldest climates of the north and west of the sampling area produced the poorest growing progeny. Although this study was primarily designed to provide data for estimation of genetic parameters such as heritability rather that uncovering geographic trends, it still showed the possible existence of north-south and east-west clines in the growth potential for white spruce.

Furnier et al. (1991) studied genetic variation in 22 populations of white spruce planted at Grand Rapids, Minnesota, using height at the ages of 9 and 19 years. They also performed electrophoresis for different allozyme loci for the same populations. Analysis of height growth showed that more that 40% of the total variance was due to differences among populations. However, variation at six polymorphic allozyme loci showed that only 3.8% of the total variability were due to differences among populations. The data for

height also showed that western and northern populations grew poorly, thus supporting north-south and east-west clines observed in other studies. To the contrary, electrophoresis data showed no geographic patterns. These apparently contradictory results from the same genetic material show that one needs to be cautious when using information obtained from genetic studies of morphological traits and those obtained with biochemical or molecular methods. The two methods are obviously measuring variation in quite different sets of genes, which might or might not be responding to the same selection pressures.

1.2.3.2 Variation in Wood Properties

In this section, wood properties of interest are wood density and tracheid length as they apply to white spruce. These properties will also be discussed on a whole-tree basis in that no distinction will be made regarding variation in wood properties for the inner or outer wood, and upper or lower part of the tree. Such specifications are considered out of the scope of this thesis.

Corriveau et al. (1987) studied wood density in 377 trees from 80 populations at seed bearing age. These populations had a range of 3° of latitude, 6° of longitude and 340m in altitude between them. It was found that 19% and 28% of the total variance in juvenile and "mature" wood density, respectively, were due to differences among populations. However, this variation showed no statistically significant geographic trend ($r = 0.29$). Taylor et al. (1982) studied wood density in four populations, two from west central Alberta (Edson) and two from northern Alberta (Footner). They found that wood density did not differ between the two forest areas (Edson vs Footner), but differed

between populations within the two forest areas. The two studies of wood properties cited above clearly suggest that genetic variation in wood density for white spruce neither show regional trends nor follow any environmental gradient similar to those observed in growth-related traits. It is unlikely that variation in wood density has survival or reproductive significance to the species. Therefore, the existence of variation in wood density among populations with no specific geographic trend might suggest that wood density in white spruce is undergoing no selection from any of environmental natural selection pressures.

1.2.3.3 Variation in Phenology

Researchers have used different traits to study genetic variation in biological rhythms (phenology) for white spruce. Blum (1988) studied bud flushing in 24 populations sampled from Alaska to Maine for three consecutive years. He found that northern populations flushed earlier than southern ones, and this trend was maintained from one growing season to another ($r \geq 0.97$). He also found that bud flushing was related to the number of degree-days above 5°C. Pollard and Ying (1979a) studied population response to declining photoperiod as measured by height growth increment accrued during the period of the study. They found large variation among families within populations but not among populations. This variation was related to the date of the first fall frost. In a follow-up study, Pollard and Ying (1979b) studied bud flushing and its relationship to late spring frost. Here too, they found large variation among families within populations but not among populations. Variation in bud flushing was related to the date of last spring frost. Thus, Pollard and Ying (1979a; 1979b) concluded that large variability among

families within populations for bud flushing and growth cessation were coadaptive strategies that enabled populations either to endure or take advantage of changes in the timing of the first fall frost and last spring frost. The lack of variation at the population level in both cases was considered to be due to the possibility that the sampled populations might have descended from the same gene pool.

Genetic variation in the timing of initiation and cessation of shoot elongation is of interest to temperate tree breeders. Specifically, breeders would like to know if the dates for budburst and budset are related to variation in annual height growth. The objective is to assess the risk of frost damage that would result from artificial selection and breeding for increased height growth. The time interval between the date for budburst and date for budset is the length of the growth period. Tree breeders would prefer families and populations whose annual shoot elongation is not related to the length of the growth period. Such populations and families would open buds late to avoid late spring frosts and set buds early to avoid early fall frosts. However, this preference can be justified if the families or populations are able to achieve adequate growth during this short growth period to provide a desired level of wood production per unit area of land. To do this, families and populations have to have high rates of growth per unit time instead of longer periods of shoot elongation.

There have been several studies supporting the dependence and independence of annual shoot elongation to the length of the growth period. In New England, Wilkinson (1977) studied budbreak for two consecutive years in 37 families collected from New Hampshire and Maine. He found that the dates for budbreak and length of the leader for the same growing season were negatively correlated genetically (year 1: $r = -0.69$ and

year 2: r = -0.94). This implies that selection for late budbreak to prevent damage from late spring frosts would lead to low annual growth. Using seed orchard clones, O'Reilly and Parker (1982) found that the annual leader length was positively correlated genetically with the duration of the growth period (r = 0.59).

The dependence of annual shoot growth on the length of the growing season has also been expressed in an impure form of white spruce. Roche (1969) studied vegetative phenology using bulk seed of 150 populations sampled from the hybrid zones of white and Engelmann, and white and Sitka spruce in British Columbia. This material is what is known as interior spruce (Stiell 1976). The study revealed that populations from higher elevation went into vegetative dormancy earlier than those from lower elevation in a clinal pattern. Except for root collar diameter, the amount of growth attained by populations depended on the number of days for active growth. The earliest populations to enter into dormancy produced the lowest dry weight.

The examples cited so far show that annual shoot growth in white spruce is dependent on the length of the growing period. However, some studies have shown the opposite to this general trend. Li et al. (1993) studied phenology and height growth in 285 families from 57 populations collected from Ontario and Quebec. They found that height growth increment was more highly correlated genetically with the rate of growth (r = 0.74±0.14) than the duration of growth (r = 0.36±0.30). The 8-year cumulative height was also more highly correlated genetically with the rate of growth observed for height increment in year 3 (r = 0.64) than the date of budset observed in year 3 (r = 0.17). Generally, the examples cited here show that with careful examination of seasonal growth rhythms, populations and families that maximise growth with less risk of frost

damage can be found. However, this would require extending indoor experiments for several growing seasons or observing field tests for many years to establish year-to-year consistency in the dates for initiation and cessation of growth. The objective of the breeder is to optimise gain through high selection differentials (Falconer 1981). Thus, even if only a small portion of the population has the appropriate combination of height growth with vegetative phenology, breeding for better growth with less risk of frost damage should be possible.

1.2.3.4 Biochemical and Molecular Variation

Despite a considerable amount of inbreeding as already discussed, white spruce retains high genetic variability in biochemical and molecular traits. For example, Rajora and Dancik (2000) found that 66% of the allozyme loci analysed were polymorphic with an average of 2.88 alleles per locus. However, the observed heterozygosity was lower than expected, pointing to possible inbreeding. Tremblay and Simon (1989) analysed 27 enzyme loci and found an average polymorphism of 76.2%. There was also a deficiency in heterozygosity. High variability of white spruce at the protein or DNA level was also reported by Mosseler et al. (1992), Furnier et al. (1991), and Furnier and Stine (1995).

1.2.4 Review on Early Selection

The term *early selection* or *early testing* as used by some tree breeders implies that selection of genotypes for establishment of seed orchards is done prior to the species' commercial rotation age (Lambeth 1980). Since rotation ages even for fast-growing tropical conifers are relatively long, all selections in forest trees apply some form of early

selection. Thus, the matter is how far should the selection age be from the rotation age. The basic question in early selection is about how much loss in gain per generation a breeder is willing to accept in order to save time (Lambeth 1980). Early selection is based on the promise that higher returns on investment that come with a reduction in testing time and costs, together with early realisation of benefits will more than compensate the disadvantages of selection at early ages (Magnussen 1988).

Early selection is a form of indirect selection in which either the trait targeted for improvement (height, diameter, volume, etc.) is selected at young ages or other traits correlated genetically with the target trait are selected. This correlated response to selection requires a strong genetic correlation between the trait being selected (juvenile trait) and the one targeted for improvement (mature trait) as demonstrated by Falconer (1981) in the following formula:

$$CR_Y = ih_X h_Y r_A \sigma_{P_Y}$$

where, CR = correlated response to selection, h = square root of the narrow sense heritability, r_A = genetic correlation between juvenile and mature traits, σ_P = phenotypic standard deviation, i = selection intensity representing the proportion of the population being selected, subscripts X and Y stands for juvenile and mature trait, respectively. The heritability and phenotypic variance depends on the genetic variability in the population from which selection is being conducted, the testing environment, and time or age at which these population parameters are estimated (Falconer 1981). In forest trees, sufficient genetic and phenotypic variability exists to guarantee acceptable heritability and phenotypic variance for selective breeding (Zobel and Talbert 1984). In addition, heritability can be increased by reducing the contribution of non-genetic variances to the

phenotypic variance through use of appropriate experimental designs and testing in the uniform environment (Zobel and Talbert 1984; Griffiths et al. 1993). The intensity of selection can be altered to increase genetic gain depending on the size of the population. Thus, the prospects of early selection as in other forms of indirect selection depend on the genetic correlation between the two traits, which is not easily manipulated.

In an attempt to shorten the breeding cycles, forest geneticists have used two approaches to obtain genetic correlations that would enable selection to be adequately performed at early stages. These methods include:

(a). Developing mathematical models to predict age-to-age genetic correlations for the same trait and decide the age at which juvenile performance best predict mature performance. This age would then become the minimum selection age. For example, Lambeth (1980) developed an empirical model for computing age-to-age genetic correlations using the published correlation coefficients in *Pinus spp* by regressing the genetic correlations on the natural logarithm of the ratio of young to old ages

$LAR = log_e (A/B)$, where:

A and *B* respectively stands for young and old age for which the correlation was computed. In this way, he obtained a predictive equation of the following form:

$$r_{AB} = c + d\ log_e (A/B)$$

where, r_{AB} is the genetic correlation for the measurements of the trait at age *A* and *B*, *c* and *d* are intercept and slope of the regression line, respectively.

This model was then used to predict genetic correlations and efficiencies of early selection for any combination of young and old ages. Lambeth (1980) showed that the

model worked well, except for genetic correlations involving very young ages. For example, the model could not predict correlations involving the age of one with subsequent ages, and correlations involving young ages were generally lower than expected from the trend revealed by correlations of later ages. This method has successfully been adopted by other researchers, e.g., McKeand (1988) and Xie and Ying (1996) to predict genetic correlations and efficiencies of early selection beyond the ages observed in the study.

Magnussen (1988) derived a model for predicting the minimum age-to-age genetic correlation between juvenile and mature ages for the same trait. This model works by computing the minimum juvenile selection efficiency and converting it to minimum age-to-age genetic correlation. The genetic correlations observed from actual field tests are then compared with this minimum correlation. Once the observed juvenile-mature correlation exceeds the designated minimum, selection done at this age would yield more gain per unit time than selection done at later ages. According to Magnussen (1988), this method is based on numerous assumptions and a difficult computational procedure, and might thus, be less attractive for practical use than the simple empirical model by Lambeth (1980). Indeed this method has hardly been used by other researchers.

(b). Searching for juvenile traits that are well correlated genetically with the mature trait of interest, especially mature height, diameter and volume per tree or hectare. These juvenile traits may be used individually or in combination (two- or more-trait selection indices) to select for a mature trait. Most of the research for the minimum selection age have been in this area and numerous juvenile traits have been recommended for use as

early selection indicators (see for example, Lambeth et al. 1983; Li et al. 1992; Xie and Ying 1996; Jonsson et al. 2000). A detailed account of the published reports for this method appears in Chapter 4. A long review of published information in this area has been excluded here to avoid repetition and conserve thesis space. It suffices to note that the decision to use one or a combination of juvenile traits may depend largely on the mature trait targeted for improvement. For example, improvement of mature height or diameter may be done well by selection for single juvenile traits such as juvenile height, diameter, branch or needle length. On the other hand, improvement of volume per hectare may require selection for a combination of traits, particularly height, diameter, survival and stem form, that is the traits from which volume per unit area is computed. Selection indices might also be necessary in situation where single juvenile traits cannot adequately predict gain in a mature trait but a combination of more than one such trait can (Falconer 1981). Selection indices may also be necessary for supplementing information obtained on mature traits with information from one or more juvenile traits that are genetically correlated with it (Falconer 1981; Wu et al. 2000).

Whichever method is used, early selection involves risks in that the gain in a mature trait predicted from selection on a juvenile trait might be less than expected (Magnussen and Yanchuk 1993). The genetic correlation between two traits expresses the extent with which the presumed two traits are genetically the same trait (Falconer 1981). This is true if the source of a genetic correlation is pleiotropic and not if the source of correlation is linkage. If the cause of correlation is pleiotropic, selection for juvenile traits imply that one is selecting for a set of genes that governs expression of both juvenile and mature traits. This is rarely true since physiological systems and gene expression change

with accumulation of size and age (Namkoong et al. 1988). In addition, the environments in which juvenile (growth chamber, greenhouse, nursery, early field studies) and mature (late field studies) traits are expressed are different such that expression of juvenile and mature traits might involve actions of quite different gene-environment interactions (Falconer 1981). In general, the closer the ages at which the juvenile and mature traits are expressed the greater the possibility that the two traits are governed by the same set of genes operating in the same environment and vice versa (Namkoong et al. 1988). This might be the reason for age-to-age genetic correlations to decline with the increase in age gap between juvenile and mature traits that is normally observed in many plant and animal experiments.

A high genetic correlation between measurement of a trait at an early stage and that of the same trait at a later stage does not necessarily mean that young and mature performances are correlated genetically. According to Lambeth (1980), the correlation between early and mature performances may exist merely due to the variance of a young trait that is part of the covariance between young and mature traits. For example, the correlation between height at an early stage (HT_A) and height at a later stage (HT_B) where the two heights are related as:

$$HT_B = HT_A + TH_I$$

TH_I being an increment accumulated between age A and B, has the following form:

$$r_{AB} = \frac{\mathrm{COV}_{AB}}{\sigma_A.\sigma_B} = \frac{\mathrm{COV}_{(A,A+I)}}{\sigma_A.\sigma_B} = \frac{\mathrm{COV}_{AA}}{\sigma_A.\sigma_B} + \frac{\mathrm{COV}_{AI}}{\sigma_A.\sigma_B} = \frac{\sigma_A^2}{\sigma_A.\sigma_B} + \frac{\mathrm{COV}_{AI}}{\sigma_A.\sigma_B}.$$

Thus, the component $\frac{\sigma_A^2}{\sigma_A.\sigma_B}$ may create the genetic correlation between early and later performance for the trait, even if the component, $\frac{cov_{AI}}{\sigma_A.\sigma_B}$, which represents the true correlation between early and later height growth is negligible. Hence, Lambeth (1980) suggested computation of the correlation between early measurement of the trait and the increment that follows to verify whether a correlation between early and later growth exists or not. It can be noted that as the gap between age *A* and *B* increases, HT_A becomes a lesser and lesser part of TH_B. Therefore, in addition to the possible change in the genes controlling the expression of a trait at young and older ages, the decline in the contribution of the variance of the juvenile trait to the covariance between juvenile and mature traits may be responsible for the decline of the age-to-age correlation as the age gap between the juvenile and mature measurements of a trait increases.

Tree height growth occurs through accumulation of annual or periodic increments, and may thus be better studied through analysis of growth increments rather than cumulative growth (Kremer 1992). Analysis of height increments can also eliminate variation in pre-planting tree size that may be connected to differences in timing for germination or seed size, and has the potential for falsely increasing the genetic variance and heritability when assessment is done shortly after planting (Burdon and Sweet 1976). The heritability of a juvenile trait is involved in the computation of the correlated response to selection (Falconer 1981), hence its overestimation due to nongenetic initial size variation will lead to high correlated response even if the two traits are not well correlated genetically. Genetic correlations among age-specific trait values describe quantitatively the link between expression of the same trait at different points in ontogeny

as the result of pleiotropy and linkage (Cheverud et al. 1983). Therefore, to better understand the genetic link between expression of height growth at different ages in the life of trees, we might have to analyse periodic increments rather than cumulative height, which is influenced by growth from previous stages. As stated by Borralho et al. (1992), the major advantage of using growth increments is that it removes from the analysis the cumulative nature of growth traits and, therefore, provide a better indication of the pattern of growth and genetic control over time.

Another factor to be considered in early selection experiments is the testing environment. Franklin (1979) suggested that testing under very close spacing would mimic the conditions under which older trees grow in forest field experiments and thus, boost the juvenile-mature correlation. Early testing studies designed to simulate conditions that limit tree growth in field experiments have been conducted. For example, in an attempt to mimic competition, Jonsson et al. (2000) tested *Pinus sylvestris* L. under wide and dense spacing, but found that phytotron-field correlations were higher at wide than dense spacing. To mimic moisture and nutrient deficiencies, Li et al. (1992) tested *Pinus taeda* L. at two contrasting moisture and nutrient combinations namely, fertilised and watered against not fertilised and not watered conditions. Juvenile-mature correlations for height were higher in watered and fertilised conditions than in the no-water-no-fertiliser condition. Correlations for stem tissue components (NSU and MSUL) showed mixed results. The test of *Pinus elliotii* Engelm. at low and high nitrogen contents produced higher correlations between 1 and 5, and 1 and 15-year heights at higher than at lower nitrogen content (Smith et al. 1993). However, stem tissue components (NSU and MSUL) produced mixed results. It appears then that simulating

field conditions in the greenhouse, growth chamber, and nursery studies may not give clear-cut results and, thus add to the confusion of pinpointing optimum selection age.

Trees in field experiments react to the interaction of many long-term climatic factors, short-term weather changes, edaphic factors, actions of other living organisms such as pest and disease agents that temporarily slows down growth of some genotypes while allowing others to grow unchecked. The magnitude of such a complicated system of interactions cannot be easily understood and manipulated. Therefore, what needs to be manipulated in retrospective studies are one or two factors that mostly limit growth in field tests.

The benefit per generation of indirect selection (including early selection) over direct selection is measured by the efficiency of indirect selection, which is the ratio of the correlated gain to gain from direct selection as follows:

$$E\,(\%) = (CR_Y/R_Y) \times 100$$

where, $E\,(\%)$ is efficiency of selection in percentage, CR_Y is correlated response in trait Y due to selection for trait X, and R_Y is response from direct selection for trait Y. In addition, efficiency of early selection can be computed per year of tree breeding effort as:

$$E_{/(year)} = (CR_Y/T_J) \div (R_Y/T_M)$$

where, T_J and T_M are times in years required for completion of the breeding cycle for the juvenile and mature traits, respectively. Detailed expressions for the efficiencies of indirect early selection are well discussed in Lambeth (1980) and in this thesis, they appear in Chapter 2.

It is important to note that computation of genetic gains from both direct and indirect selection includes heritability values of the traits involved. As already mentioned,

correlated gain involves also the genetic correlation between the two traits. As stated elsewhere (see, e.g., Chapter 4) heritabilities for juvenile traits, especially tree seedling height tend to be higher than heritabilities for advanced-age field-height. In this case, correlated gains and the resulting efficiencies of early selection may be high even if the juvenile-mature genetic correlations are low. Therefore, to insure that gains predicted from selection on a juvenile trait will be realised in a mature trait, a high genetic correlation is necessary to offset the effect the declining heritability with age of the trait being selected will have on the correlated gain. Although there is no clear definition of what constitutes a low or high genetic correlation, Namkoong et al. (1988), indicated that a correlation of 0.6 is still low. However, for naturally early flowering species or for species in which early flowering can be easily induced through various reproductive technologies, a low genetic correlation can help to shorten the breeding cycle through early selection (Namkoong et al. 1988). Therefore, in late maturing species, the general rule could be that when a high heritability for a juvenile trait cannot be assumed in the long-term, a very high genetic correlation should be sought. On the other hand, if a high heritability for the juvenile trait can be maintained in the long term, early selection at young ages can still be efficient even with low and medium genetic correlations.

A caution should be made here in the interpretation and use of gain per year rather than gain per generation of tree breeding. Early selection tends to be much more efficient in gain per year than selection at later stages (Lambeth 1980, Xie and Ying 1996), especially when the age required for early selection (T_J) is much lower than the age required for selection of a mature trait (T_M). Thus, when T_J and T_M are on the opposite extremes, gain per generation is a better criterion for judging the efficiency of early

selection than gain per year. With extreme T_J and T_M, gain per year from early selection will be several times larger than gain per year from direct selection of the mature trait, thus creating a false or unrealistic impression.

The genetic correlation is computed from three estimators, i.e., the covariance of the two traits and variances of individual traits (Falconer 1981). Therefore, they tend to have higher standard errors than it would be the case if they were computed from fewer estimators (Namkoong et al. 1988). It has been stated that in addition to other benefits, early selection promises smaller genetic tests (Magnussen 1988; Lambeth 1980), as it would be the case in controlled environments. However, small tests imply high standard errors for both the heritability and genetic correlation values, since the standard error of the estimate increases with the decrease in sample size. In a simulation study, Magnussen and Yanchuk (1993) demonstrated that for early family selection, reduction in the optimum selection age would require increases in the number of trees per family involved in the test. In this case, at least 20 and more than 40 trees per family would be needed in the test if selection were to be done with less risk before age 10 and 15 years, respectively. However, increasing the number of trees per family reduces the number of families included in the progeny test. This is true even in studies involving single-tree plots. Thus, always there will be risks in early selection programmes that breeders need to be aware of and try to minimise them accordingly.

In conclusion, early selection has its own uncertainties that are born in the large difference between the length of commercial rotation age and the waiting time before selection, which the tree breeder can economically and biologically justify. Despite these uncertainties, early selection is inevitable even in species considered fast growing such as

tropical pines or Eucalypts. Hence, every effort should be made to devise reliable early selection criteria. These could be early and easily measurable morphological, physiological and biochemical traits, or could involve the use of biotechnology to identify superior genotypes for metric economic traits at the seedling or sapling stage.

CHAPTER II: MATERIAL AND METHODS

2.1 Description of the Test Material

The families used for this study in the greenhouse and in the field were collected from trees that were chosen because of their good phenotypes, namely tall trees with straight bole, right-angled branches and free of disease or insect damages. Seed collection was done between 1979 and 1983. The sampled region is within the Peace River Basin, northwestern Alberta, Canada, between latitude 54°31' and 58°03' N, longitude 117°35' and 119°22' W and 365-945 metres above the sea level. All families originated from open-pollinated seed collected without population structure. A total of 69 families were collected but only 58 were used in this study. It was assumed that these families are representative samples of the species fully adapted to the forest environments in Peace River Basin as represented by the two long-term tests described in section 2.2.1.

2.2 Experimental Procedures

2.2.1 Field Trials and Assessment

In 1988, Alberta Lands and Forest Service established two field trials under the project title *White spruce progeny testing for region G.* These field trials are located at Chinchaga River and Saddle Hills experimental areas as described bellow:

1. Chinchaga River Genetics Experimental Area (G135A) is located at 57°50' N, 118°12' W and 470m above sea level. The soil can be classified as 80% well drained with poorly drained soil pockets constituting the remaining 20%. Soil pH was between 6.5 and 7.5. The site was originally a dense aspen stand. In this thesis, this progeny trial is referred to as site A.

2. Saddle Hills Genetics Experimental Area (G135B) is located at 55°31' N, 119°40' W and 914 m above sea level. The soil is generally a mixture of silt, loam and clay, which is better drained than site A. The original stand was a mixture of spruces, pines, and aspen. In this thesis, this progeny trial is referred to as site B.

At the time of field planting, seedlings were 4-years old. The experimental design was a randomised complete block with 6 replications and 6-tree row plots. A 2.5m x 2.5m spacing between trees was adopted at both field test sites. Both field trials were assessed for height growth at 10 and 11 years from seed. It is this height growth assessment that will be used in this thesis to establish genetic correlation coefficients with various traits in a retrospective study described in the next section.

2.2.2 The Greenhouse Retrospective Study

The growth medium for the greenhouse phase of the study was a 2:1 parts peat to vermiculite mixture with 5.0g/litre of lime added to bring the pH to about 5.0. Both seed germination and seedling growth were conducted in 700ml styroblocks with 20 cavities per block. Prior to pot filling, all styroblocks were sterilised by soaking them in a 0.5% solution of household bleach and then rinsed in tap water to remove factory impurities.

Sowing was done for two consecutive days during the first week of April 1996 in the greenhouse at the University of Alberta in Edmonton. Prior to sowing, the seeds were cold stratified at 2°C for 21 days by the staff of the Alberta Tree Improvement and Seed Centre at Pine Ridge. Seed germination was complete two weeks after sowing. When germination was complete, seedlings were transplanted leaving only one seedling per cavity. For plots where germination did not take place, seedlings from plots of the same

family with multiple germinants were brought in to fill the gaps. Families 16 (2053), 38 (2463) and 41 (2466) had poor germination and less than the 30 seedlings required per family. All other families were fully planted at the beginning of the experiment.

The design of the experiment was a randomised complete block with non-contiguous single-tree plots, 30 replications (blocks) and 58 open-pollinated families. With this design, each tree in the block represented a different family. Families were randomly assigned to the styroblock cells and each block was randomised independently. Each plot was tagged with the family number throughout the testing period to preserve identity.

Throughout the experiment, the greenhouse compartment was set at 23°C day and night, except during the hardening period when the temperature was reduced by 2°C every week to bring about complete rest before the seedlings could be taken outside the greenhouse for over-wintering. These temperature reductions did not go below 14°C. However, the greenhouse used was not designed to control heat from outside the compartment. During hot sunny days, temperature in the compartment would rise far beyond 23°C depending on the daily maximum temperature. Thus, the 23°C constancy could be maintained only during the night and on cloudy or rainy days. Seedlings were raised at an extended photoperiod of approximately 20 hours a day. This included natural spring and summer light supplemented by 6 hours of artificial light. The 400w sodium bulbs on Sylvania fixtures hanging above the seedlings generated this artificial light. The light intensity was estimated at $450\mu mol\ m^{2}sec^{-1}$ (maximum) (Bruce Alexander 1996 pers. comm.). On sunny days, the artificial light was provided during the period between 8.00 p.m. and 2.00 a.m. During cloudy or rainy days, artificial light was supplied for the

entire 20-hour daily growing period. In addition, artificial light was used whenever natural light was judged to be of too low intensity to insure normal seedling growth.

At the start of the experiment, seedlings were watered twice a day. As seedlings became well established and the growth media water-saturated, watering was reduced to once per day. Thereafter, watering was done every two days depending on the weather conditions. The general fertilisation schedule was once a week, with the fertiliser being applied in solution during the routine Monday morning watering. The nutrient ratios used for the growing and hardening periods were those prescribed for pine and spruce seedlings by the Alberta Tree Improvement and Seed Centre at Pine Ridge. They are reproduced here in terms of concentration (gm/litre) as follows:

(a) *Grower fertiliser mix*:

Calcium nitrate 15.5-0-0 (37.89 g/l), Potasium nitrate 13-0-44 (49.90 g/l), Monopotasium phosphate 0-52-34 (57.45 g/l), Magnesium sulphate (68.8 g/l), Amonium nitrate 18.82 g/l), **Micronutrients:** Iron chelate (3.81g/l), Manganese chelate (0.62 g/l), Copper chelate (0.56 g/l), Sodium molybdate (0.03 g/l), Zinc chelate (0.15 g/l), Borax (0.21 g/l).

(b) *Hardening fertiliser mix*:

Calcium nitrate 15.5-0-0 (40.42 g/l), Potasium nitrate 13-0-44 (12.67 g/l), Monopotasium phosphate 0-52-34 (57.45 g/l), Magnesium sulphate (64.00 g/l), **Micronutrients:** Iron chelate (4.82g/l), Manganese chelate (0.62 g/l), Copper chelate (0.56 g/l), Sodium molybdate (0.03 g/l), Zinc chelate (0.15 g/l), Borax (0.21 g/l).

In the first growing season, application of fertiliser started 20 days after seed sowing or 6 days after transplantation of the seedlings. In the second and third growing seasons, fertilisation started when 80% of the seedlings had opened buds. During the first and second growing seasons, application of hardening fertiliser started at the end of the last week of July, and ended at the beginning of September, when the seedlings were taken out of the greenhouse for over-wintering.

At the end of both the first and second seasons, seedlings were moved out of the greenhouse to the roof of the Agriculture and Forestry Building at the University of Alberta for over-wintering. Seedlings were well watered and thereafter over-wintered until the last week of April or first week of May of the following year. Thereafter seedlings were returned to the greenhouse.

Different traits were assessed from the seedlings for all three growing seasons, but most of these traits were assessed during the second season. Some of these traits were used to derive other traits that will be encountered in the thesis. Traits that were directly measured from the seedlings and the growing season when they were assessed are described as follows.

Stem height: Nine (9) measurements of total seedling heights were taken every 14 days in each of the first and second growing seasons. In the third growing season, only five (5) measurements of total seedling height were taken, since seedlings stopped growing much earlier in the season. Thus, a total of 23 measurements of total seedling heights were taken during the entire greenhouse phase of the study. However, during the third season, many seedlings suffered terminal diebacks after over-wintering and, therefore could not sustain height growth on the main leader.

Thus, for this thesis, analysis and reporting is restricted to the first and second season height assessments.

Root collar diameter: Three (3) measurements of root collar diameter were taken every 6 weeks during the second growing season, and only one (1) measurement was taken at the end of the third growing season. An electronic calliper was used for all root collar diameter measurements.

Branch length: At the end of the second growing season, the three longest branches were identified and their length measured from base to tip.

Number of buds: When seedlings were brought back into the greenhouse at the beginning of the second growing season, many buds were formed on the main stem. These buds were counted for future analysis. Since such buds tend to grow into branches, existence of the genetic variance for the number of buds would indicate the potential for branchiness in the tested families.

Number of Branches: The number of branches was assessed at the end of the second growing season. Fully developed branches were counted only in the first season segment of the seedlings. At the beginning of the second season, it was observed that, many branches in the first season segment of the seedlings elongated from lateral buds, which opened at the beginning of the second season. For this reason, branches were not counted in the second season segment of the seedlings, since it was expected that many branches in this part of the seedlings would be formed during the third growing season. Also, branches in the second season segment of the seedling could not be counted at the end of the third season, since many seedlings suffered terminal dieback due to over-wintering after the second season.

Needle length: In the middle of the second growing season, 10 mature needles were plucked at random from the first season's portion of the oldest branches. The lengths of these needles were measured from base to tip.

Budburst date: The dates for opening of the lateral and terminal winter buds were recorded for each seedling at the beginning of the second and third growing seasons. A seedling was considered to have opened bud on that day when the scale protecting the terminal bud ruptured to expose needles not later than 6:00 p.m. of that day. Assessment of budburst dates was done everyday between 3:00 and 6:00 p.m. At the beginning of the second season, it was noted that buds on branches and lateral buds on the main stem tended to open earlier than the terminal bud on the main stem. Thus, in addition to the date for budburst of the terminal bud, the budburst date for the majority of buds on branches and lateral buds on the main stem was recorded. This would provide a tentative assessment of budburst dates especially in seedlings whose terminal budburst was seriously delayed. Data analysis for budburst was performed on the number of days from movement of seedlings back into the greenhouse to the day when budburst occurred.

Stem Shoot Components: In this thesis, stem shoot components refers to the number of stem units (NSU) and mean stem unit length (MSUL) as defined by Doak (1935). The two can simply be referred to as the number of needles and the mean length between these needles, respectively. At the beginning of the third growing season, needles were extracted from the second season's portion of the two longest branches for all seedlings, which had shown adequate growth in the second

season and which had retained healthy branches and needles after over-wintering. NSU in this portion of the branch was initiated during the first growing season and could, therefore, provide a measure of the extent to which NSU and MSUL determined the length of the branch achieved in the second season. In addition, correlation coefficients could be computed for each of NSU and MSUL with total branch length accrued over two seasons, total seedling height accrued over two seasons and the second seasons height growth for the main stem. The harvested needles were counted to obtain the NSU, whereas the segment of the branch from which the NSU was determined was measured to obtain the stem length (SL). MSUL was derived as the ratio of SL to NSU. Tissue components were assessed from the branches and not the main stem to avoid damage to the main stem, since the Alberta Forest Service had earlier planned to transplant the seedlings to a field experiment once the greenhouse study was completed.

Biomass Production: Biomass pro[illegible]n was assessed for all seedlings, which did not lose much of their vegetative part during over-wintering and whose growth in the third season reflected the overall growth of the experiment. Seedlings were harvested and partitioned into branches, main stem, and the roots. Due to the lack of a well-developed taproot system, it was not possible to further partition the root system into lateral and taproot systems as previously planned. The roots were washed in tap water to remove soil particles and air-dried for 24 hours before being transferred into an oven for further drying. Prior to oven drying, branches and main stems were measured to determine their fresh weight. Fresh weight for the root system was considered irrelevant in this case, since it would be more

influenced by external water than water in the intercellular spaces as the result of washing. All plant parts were then oven-dried to constant weight at 110°C for 72 hours.

2.3 Data Analysis

2.3.1 Modelling of Stem Height Growth

2.3.1.1 First and Second Season Growth Curves

One of the main objectives of this thesis was to study the pattern of seasonal height growth for the main stem under greenhouse conditions, and use the derived traits for genetic analysis and early selection to improve field height growth. This involved the analysis of the growth curves that described the overall growth paths of the seedlings during the first and second growth periods. It should be made clear here that growth curve analysis for the first season involved study of height growth starting from seed germination to the onset of dormancy at the end of the first season following the initiation of the experiment. In contrast, growth curve analysis for the second season involved study of the height increment accrued from the time of budburst at the beginning of the second season to the time of budset at the end of the same season. Therefore, in generating second season height increments, the final cumulative height reached at the end of the first season was deducted from all biweekly height measurements recorded during the second season. This distinction is important especially in the interpretation of the genetic correlations between greenhouse and field height later in the thesis. In this case, correlations between first season height and its growth curve derived traits with field height will be age-to-age correlations, whereas the corresponding correlations

involving second season height and its growth curve derived traits will not. This section describes the procedure used in the choice of the growth model and the traits derived from the model for further analysis.

2.3.1.2 Choice of the Growth Model

The criteria used in the choice of the growth model was that the model should adequately describe growth that took place, the model should not be biased in describing that growth, parameters (functions) of the model should have biological meaning and fit well in the genetic selection and plant breeding subject which is the topic of this thesis. In studying seasonal growth curves, the main interest was to be able to describe families in terms of their rates of growth and the length of their period of growth. By plotting the original data, it was noted that in both the first and second growing seasons, height growth for the main stem was sigmoid in shape and this growth pattern was more pronounced during the first than the second growing season. With this type of growth, curve parameters that were of interest are the rate of growth, the time at the point of inflection, and the extrapolated height. In this case, the time at the point of inflection would provide the measure of the duration of growth.

Four growth models were evaluated for their fit to the data and the results appear in Table 1. These models are described as follows:

Using seedling height, parameters represented by similar symbols in the simple logistic, generalized logistic (Nalder 1961), and Gompertz models are defined as follows:

W = seedling height at time t, A = upper asymptotic height, b = function representing the choice of the initial height or time zero (Richards 1959), r = growth rate, t = time, e =

base of the natural logarithm. In the generalized logistic model, λ is the constant of integration and θ shows the type of the model, i.e., depending on the value of θ, the generalized logistic model (Table 1) might be equivalent to simple logistic, Gompertz, and many other models (Nalder 1961).

Dr. Run-Peng Wei while working as a Research Associate in the Department of Renewable Resources at the University of Alberta proposed the model that I have here called "Wei". He described the items in this model as follows:

S = shoot elongation at time T (equivalent to W in the other three models),

C = growth capacity (equivalent to A in the other three models),

V and W = shape parameters,

T_h = time at $1/2C$ (or time at the point of inflection),

T_P = period of elongation from zero to zero (equivalent to the length of the growing season).

This model has not yet been published by its author and, therefore, it will not be discussed any further in this thesis. Its presence in this thesis only helps to show that the greenhouse data used in this thesis fit well a variety of mathematical models used to describe the sigmoid type of growth.

These four mathematical models were fitted to the data using the *Gauss-Newton* method in the nonlinear model procedure (PROC NLIN) in the SAS software version 8. To obtain the goodness of fit for the model to the data, the predicted height values of individual seedlings were regressed on the corresponding observed values. The coefficient of determination (r^2) from this regression was then used to judge the goodness of fit for the model. To assess the bias of the model, residues (*observed* minus *predicted*

value) were plotted and regressed against time and predicted values. In this case, the good model should predict height fairly at all seedling ages without predicting lower values at certain ages and higher values at other ages. Similarly, the model should fairly predict height for all seedling size classes without overestimating predicted height for seedlings of certain size classes and underestimating that of other size classes. In other words, both the plots of residues against time and residues against predicted values should show no pattern. The results from the model evaluation process appear in Table 1. Note that all four models fitted the data well, especially the first season ones. The Wei model converged for the second season data, but the results appear to be unreasonable for a significant proportion of the seedlings.

Table 1: Test for the goodness of fit for the different growth models to the first (regular font) and second (bold font) season data

Model Author or Name	Equation	Coefficient of determination (r^2)		
		Predicted on observed	Residues on Predicted	Residues on time
Simple Logistic	$W = \frac{A}{1+be^{-rt}}$	0.9980	0.0147	0.0380
		0.9940	**0.0450**	**0.0846**
Gompertz	$W = Ae^{-be^{-rt}}$	0.9930	0.0267	0.0571
		0.9900	**0.0038**	**0.0123**
Generalized Logistic (Nalder 1961)	$W = \frac{A}{(1+e^{-(\lambda+rt)/\theta})^{\theta}}$	0.9990	<0.0001	0.0002
		0.9970	**0.0001**	**<0.0001**
Wei	$S = \frac{C}{1+(1-\frac{T}{T_P})e^{[(-\frac{(T-T_h)}{W})+(\frac{T}{T_P})(\frac{T}{T_h})^r]}}$	0.9970	0.0129	0.0018
		NA	**NA**	**NA**

NA = Not available because the model did not adequately converge for most of the second season data

The excellent fit for the simple logistic and the generalized logistic (Nalder 1961) models suggests that the overall growth pattern of the seedlings followed the logistic function. Thus the simple logistic model was chosen for genetic analysis. This choice is based on the following reasons:

1. The model has only three parameters to be estimated and, therefore, parameters were estimated with small asymptotic standard errors given that only nine periodic measurements were made. The size of the standard errors for the parameters is expected to increase with the increase in the number of parameters in the model.
2. In addition to nonlinear regression, there are other methods of fitting the simple logistic model that use either all nine data points or only three selected data points without losing accuracy in predicting the periodic height and estimating the parameters. These methods were suggested by Nair (1954). As will be seen later in the results chapter, these methods were very useful in comparing some of the genetic correlations from the second season growth curves with those from the first season that were not easily comparable by nonlinear regression results. These methods of fitting the simple logistic curve without undertaking iterative nonlinear regression will not be reviewed in this thesis. However, since these methods were used together with nonlinear regression, interested readers are referred to the *methods of sums of reciprocals* and the *method of selected points* in Nair (1954).
3. With all models fitting equally, it is imperative to choose the simplest one.

2.3.1.3 The Simple Logistic Model

This section introduces briefly the simple logistic model and the symbols that are used in the rest of the thesis as far as the growth curve analysis is concerned. It also presents the plots and regressions for the residues on time, residues on predicted values and predicted values on observed values that were generated during the evaluation of the simple logistic model.

The logistic function fitted in this study with seedling height (h_t) as a response trait at time t is of the form:

$$h_t = \frac{k}{1+be^{-rt}}$$

where k is upper asymptotic height or h at $t=+\infty$, r is the rate of growth, b is a constant representing the choice of time zero and it has no biological value (Richards 1959), t is time in days, and e is the base of the natural logarithm. The logistic function has the point of inflection midway between the upper and lower asymptotic height or *1/2k*. Thus the time at the point of inflection is the time corresponding to the point $(\frac{1}{r}\log_e b, \frac{1}{2}k)$ on the growth curve and because of its association with *1/2k* it is denoted in this thesis as $t_{0.5}$ computed as follows:

$$t_{0.5} = \frac{1}{r}\log_e b$$

The parameter k, b and r were estimated directly from the data by three methods namely, *nonlinear regression* (PROC NLIN in SAS software), *method of sums or reciprocals* (Nair 1954) and *method of selected points* (Nair 1954). Notice that the first two methods used all nine data points at two-week intervals whereas the method of selected points used the first, fifth and ninth data points to fit the logistic function. The plots presented

here (Figure 1 through Figure 10) are those from the nonlinear regression and the method of selected points. This is meant to show that the model fits well the data when all nine data points are used and also when only three representative data points are used. Figure 10 shows some trend in the residues for the second season data when fitted by the method of selected points. This is because the method of selected points tended to overestimate the predicted height for seedlings with observed height of greater than 200 millimetres. However, these seedlings represent a very small fraction of the data and should be ignored. Also as we shall see later when we deal with genetic correlations, the method of selected points produced the most reasonable results for the second season data when compared with the other two methods.

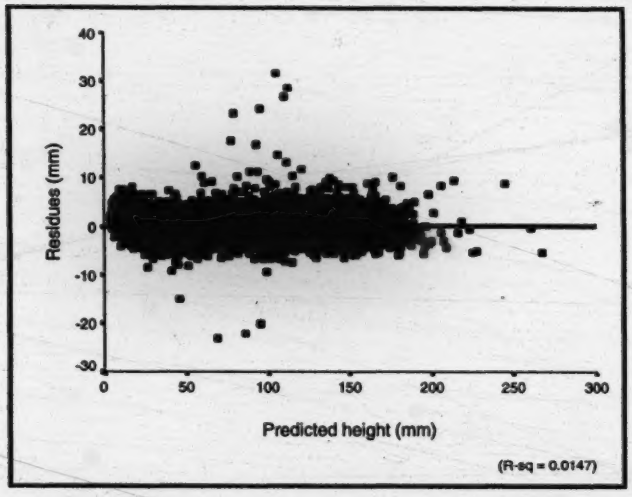


Fig. 1: Scatter plot and the regression of the residues on predicted height for the first seasons data based on the simple logistic model

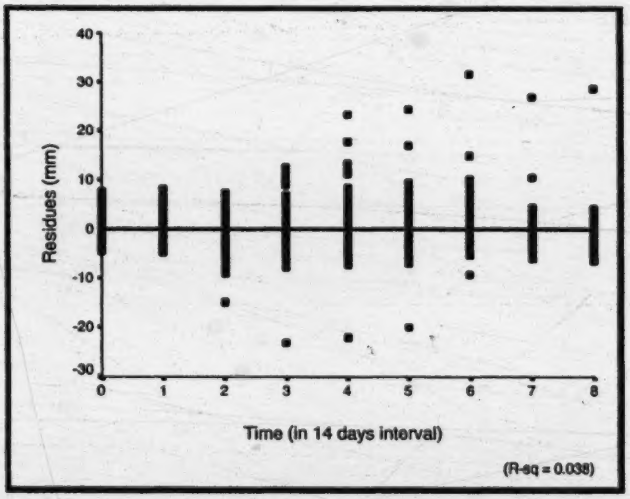


Fig. 2: Scatter plot and the regression of the residues on time for the first season data based on the simple logistic model.

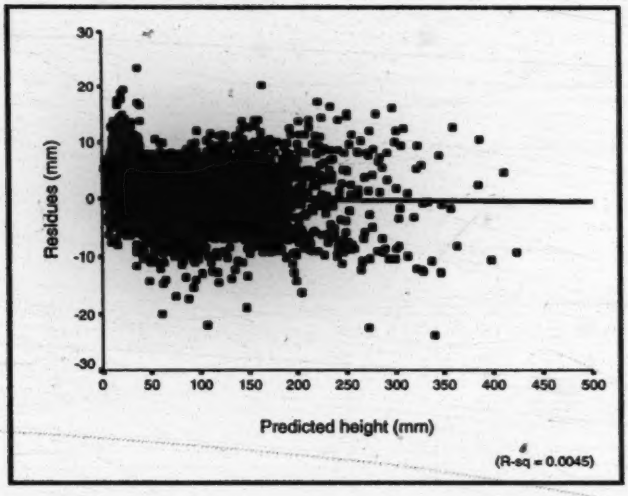


Fig. 3: Scatter plot and the regression of the residues on predicted height for the second season data based on the simple logistic model.

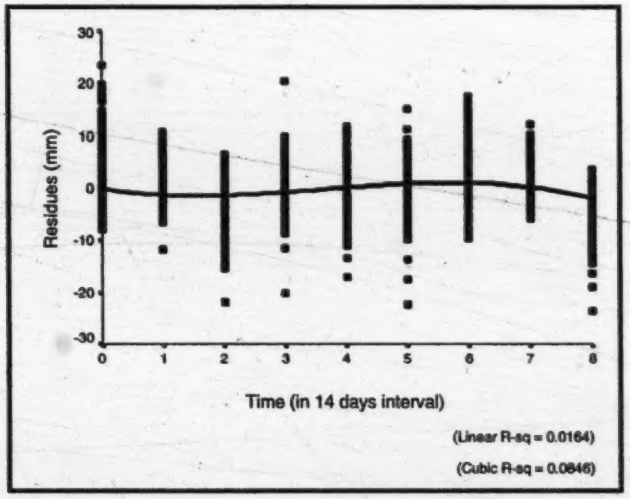


Fig. 4: Scatter plot and the regression of the residues on time for the second season data based on the simple logistic model.

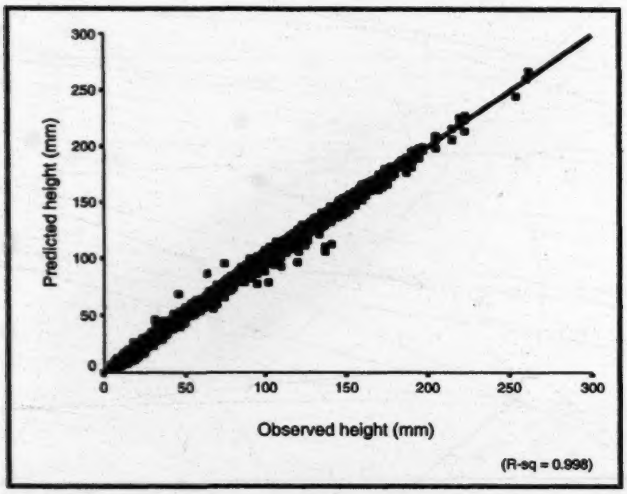


Fig. 5: Scatter plot and the regression of predicted height on observed height for the first season data based on the simple logistic model.

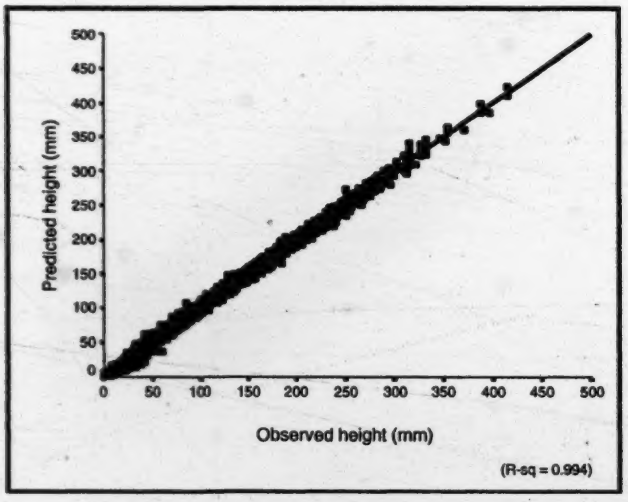


Fig. 6: Scatter plot and the regression of predicted height on observed height for the second season data based on the simple logistic model.

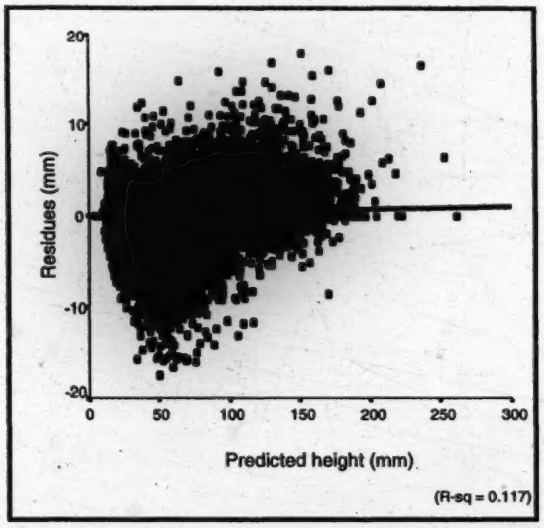


Fig. 7: Scatter plot and the regression of residues on predicted height for the first season data based on the simple logistic model fitted by the method of selected points

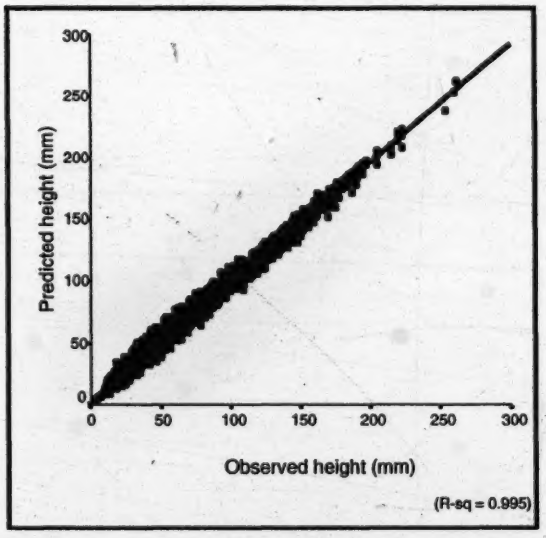


Fig. 8: Scatter plot and the regression of predicted height on observed height for the first season data based on the simple logistic model fitted by the method of selected points

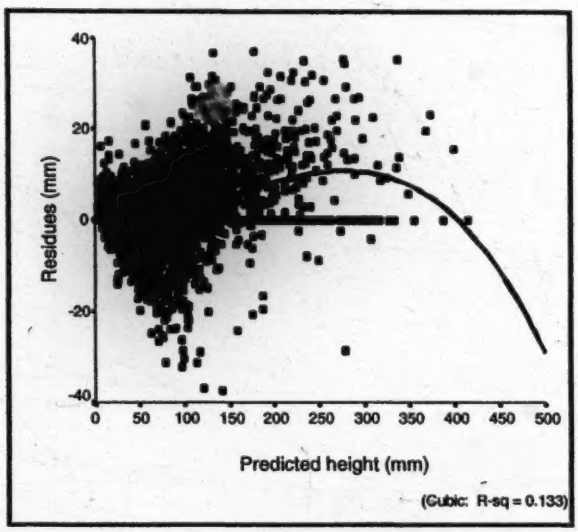


Fig. 9: Scatter plot and the regression of residues on predicted height for the second season data based on the simple logistic model fitted by the method of selected points.

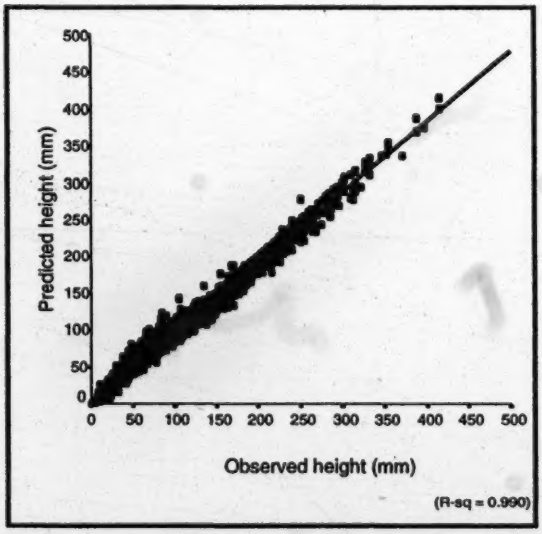


Fig. 10: Scatter plot and the regression of predicted height on observed height for the second season data based on the simple logistic model fitted by the method of selected points

2.3.2 Genetic Analysis

2.3.2.1 General Analysis for Greenhouse Data

This section describes the analytical procedures that were used to analyse all greenhouse-assessed traits except the tissue components, i.e., NSU and MSUL. A slightly different model and procedure was employed in analysing the tissue components. Thus, analysis of tissue components will appear in a separate section. Traits k, r and $t_{0.5}$ from the growth curve analyses and all other greenhouse-measured traits were checked for conformity to the normal distribution and the homogeneity of the error variance assumptions. All traits were then square-root transformed to achieve normality and stabilise the residual variance. The statistical model used to analyse most of the greenhouse-measured data was:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$$

where,

Y_{ij} = response due to the j-th family planted in the i-th block,

μ = general mean,

α_i = effect due to the i-th block or replication, $IND\ (0,\ \sigma^2_\alpha)$,

β_j = effect due to the j-th family, $IND\ (0,\ \sigma^2_\beta)$,

ε_{ij} = error (residual) associated with the j-th family in the i-th block,

$IND\ (0,\ \sigma^2_\varepsilon)$.

Except for the mean, all items in the right side of the model were considered independent, additive, random, and normally distributed with zero expectation (mean) and respective variances as indicated in the parentheses. The ANOVA for this model appears in Table 2.

All analyses of variance were performed with the General Linear Model Procedure (SAS 1994) with Type IV sums of squares. The use of Type IV sums of squares was necessary due to the design of the greenhouse experiment. When experimental plots are made up of single trees, every missing tree represents a missing cell. Therefore, Type IV sums of squares were relevant for the validity of statistical tests (SAS 1994).

Table 2: Analysis of variance and covariance for analysing the greenhouse data

Source	df	Expected Mean Squares	Expected Mean Cross Products
Block	$\alpha-1$	$\sigma_\varepsilon^2+k_\alpha\sigma_\alpha^2$	$\sigma_{\varepsilon_1\varepsilon_2}+k_\alpha\sigma_{\alpha_1\alpha_2}$
Family	$\beta-1$	$\sigma_\varepsilon^2+k_\beta\sigma_\beta^2$	$\sigma_{\varepsilon_1\varepsilon_2}+k_\beta\sigma_{\beta_1\beta_2}$
Error	$\alpha\beta-1$	σ_ε^2	$\sigma_{\varepsilon_1\varepsilon_2}$

α, β, ε, indicates block, family and error, respectively

Using the symbols defined in Table 2, the individual tree heritability was computed as:

$$h_i^2=\frac{3\sigma_\beta^2}{\sigma_\varepsilon^2+\sigma_\beta^2}$$

where h_i^2 is the individual-tree heritability. Due to considerable inbreeding and lack of inbreeding depression in young white spruce seedlings (Fowler and Park 1983, Park et al. 1984), the between-family variance component was multiplied by 3 instead of 4 to obtain the additive genetic variance for computation of individual tree heritability. The standard error of the individual-tree heritability was estimated according to Becker (1975). The heritability for family means was computed as:

$$h_f^2 = \frac{\sigma_\beta^2}{\frac{1}{k_\beta}\sigma_\varepsilon^2 + \sigma_\beta^2}$$

where h_f^2 is heritability for family means. The standard error for the heritability for family means was computed according to Wright (1976).

Genetic, phenotypic and environmental correlation coefficients were computed by substituting the appropriate covariance and variances for any two traits into the following general formula:

$$r_{xy} = \frac{\sigma_{xy}}{\sigma_x . \sigma_y}$$

where $r_{xy} = r_{A_{XY}}$, $r_{P_{XY}}$, $r_{E_{XY}}$ for genetic, phenotypic and environmental correlation coefficients, respectively; $\sigma_{xy} = \sigma_{\beta_{XY}}$, $\sigma_{P_{XY}}$, $\sigma_{\varepsilon_{XY}}$ for genetic, phenotypic and environmental covariance components, respectively; σ_x and σ_y are respectively, σ_{β_X} and σ_{β_Y} for genetic, σ_{P_X} and σ_{P_Y} for phenotypic, and σ_{ε_X} and σ_{ε_Y} for environmental standard deviations for the two traits. Standard errors for the genetic correlation coefficients were computed according to Robertson (1959).

2.3.2.2 Analysis for Tissue Components

This section describes the procedure used in analysing the extent with which the number of stem units (NSU) and mean stem unit length (MSUL) jointly determined the second season's branch increment. This analysis involved only families represented by at least 5 seedlings (10 observations). The number of families was 53 and the total number of

seedlings was 555 or 1110 observations, since each seedling was represented by two branches. The statistical model used in analyzing tissue components was:

$$Y_{nj(i)} = \mu + \beta_i + \gamma_{j(i)} + \varepsilon_{nj(i)}$$

where,

$Y_{nj(i)}$ = n-th observation on j-th tree within i-th family,

μ = general mean,

β_i = effect due to i-th family, *IND* $(0, \sigma^2_\beta)$,

$\gamma_{j(i)}$ = effect due to j-th tree within the i-th family, *IND* $(0, \sigma^2_\gamma)$,

$\varepsilon_{nj(i)}$ = error, *IND* $(0, \sigma^2_\varepsilon)$,

All terms on the right side of the model were considered random, additive, independent and normally distributed with zero expectation and variances as indicated in the parenthesis. The ANOVA for this model appears in Table 3.

Table 3: Analysis of variance and covariance for greenhouse tissue components (NSU and MSUL)

Source	df	Expected Mean Squares	Expected Mean Cross Products
Family	β-1	$\sigma^2_\varepsilon + k_3\sigma^2_\gamma + k_4\sigma^2_\beta$	$\sigma^2_{\varepsilon_1\varepsilon_2} + k_3\sigma^2_{\gamma_1\gamma_2} + k_4\sigma^2_{\beta_1\beta_2}$
Tree(Fam)	$\beta(\gamma$-1)	$\sigma^2_\varepsilon + k_1\sigma^2_\gamma$	$\sigma^2_{\varepsilon_1\varepsilon_2} + k_1\sigma^2_{\gamma_1\gamma_2}$
Error	$\beta\gamma n$-1	σ^2_ε	$\sigma^2_{\varepsilon_1\varepsilon_2}$

β, $\gamma$and ε, indicate family and tree-within family and error, respectively

In addition to the variances, heritability and correlation coefficients, the degree of joint determination of the second season's branch length increment (SL) by NSU and MSUL was estimated using the path coefficient analysis. The genetic correlation coefficient can only tell us the extent to which NSU or MSUL individually vary with SL. Only the path coefficient analysis can tell us the extent to which NSU and MSUL together determine SL. Kremer and Larson (1983) and Bongarten (1986) well described the use of path coefficients analysis in the study of stem tissue components in *Pinus* spp. Briefly, the method works as follows:

Since SL = NSU x MSUL (1)

log (SL) = log (NSU) + log (MSUL) (2)

If NSU and MSUL are correlated, then

var ((SL)) = var (log (NSU)) + var (log (MSUL)) + 2 cov ((log (NSU), log (MSUL)) (3)

If we use x, y, and z to represent parts of the above equations to indicate SL, NSU and MSUL, respectively, and use Greek script, equation 3 is equivalent to equation 4 below

$$\sigma_x^2 = \sigma_y^2 + \sigma_z^2 + 2\sigma_y\sigma_z r_{yz} \quad (4)$$

Where r_{yz} = the correlation coefficient between NSU and MSUL.

By dividing each part of the equation by the total variance (σ_x^2), i.e., the variance due to SL, we obtain equation 5.

$$p_x^2 = p_y^2 + p_z^2 + 2p_y p_z r_{yz} \quad (5)$$

where,

p_x = the path coefficient for log (SL) to itself, thus $p_x = 1$,

p_y and p_z are, respectively, the path coefficients for log (NSU) and log (MSUL) to log (SL).

When SL, NSU and MSUL are standardised, the relative contributions of NSU and MSUL to SL are, respectively, computed as follows:

$$c_y = p_y r_{xy} \text{ and } c_z = p_z r_{xz}$$

Where c_y and c_z are, respectively, the relative degree of determination of SL by NSU and MSUL, r_{xy} is the correlation coefficient between SL and NSU, and r_{xz} is the correlation coefficients between SL and MSUL.

Notice that $c_y + c_z = 1$

Before performing the analyses of variance, the data for SL, NSU and MSUL were standardised by dividing each trait to by mean. This makes it possible for the variances to be compared when computing the path coefficients, since by standardisation each trait has a mean of 1 (Bongarten 1986). It also facilitates the estimation of degree of determination of SL by NSU and MSUL (Kremer and Larson 1983). However, when divided by their mean, data points that were originally below the population mean acquired a value of less than 1, leading to negative logarithms. To prevent negative logarithms, I added a constant 1 to all data points for all standardised SL, NSU and MSUL prior to taking the logarithms. To ensure that standardisation did not change the amount of variation that existed in the original units, the variance components, heritability and correlation coefficients were computed for both unstandardised and standardised data.

2.3.2.3 Analysis of Field Data

Field data for computing correlations with greenhouse data were available for two test sites. Each site was analysed individually using the following statistical model:

$$Y_{n(ij)} = \mu + \alpha_i + \beta_j + \alpha_i\beta_j + \varepsilon_{n(ij)}$$

where,

$Y_{n(ij)}$ = response on n-th tree in the i-th family and j-block,

μ = general mean,

α_i = effect due to i-th block, *IND* $(0, \sigma^2_\alpha)$,

β_j = effect due to j-th family, *IND* $(0, \sigma^2_\beta)$,

$\alpha_i\beta_j$ = effect due to family by block interaction, *IND* $(0, \sigma^2_{\alpha_i\beta_j})$,

$\varepsilon_{i(ij)}$ = error, *IND* $(0, \sigma^2_\varepsilon)$,

All terms in the right side of the model were considered random, additive, independent, and normally distributed with zero expectation and variances as indicated in the parenthesis. The ANOVA for this model appears in Table 4.

Table 4: Analysis of variance for field height.

Source	df	Expected Mean Squares
Block	α-1	$\sigma^2_\varepsilon + k_4\sigma^2_{\alpha_i\beta_j} + k_5\sigma^2_\alpha$
Family	β-1	$\sigma^2_\varepsilon + k_2\sigma^2_{\alpha_i\beta_j} + k_3\sigma^2_\beta$
Block*family	(α-1)(β-1)	$\sigma^2_\varepsilon + k_1\sigma^2_{\alpha_i\beta_j}$
Error	$\alpha\beta n$-1	σ^2_ε

α, β, ε, indicate block, family and error, respectively

Heritability for field height were computed according to the following equations:

$$h_i^2 = \frac{4\sigma_\beta^2}{\sigma_\varepsilon^2 + \sigma_{\alpha_i\beta_j}^2 + \sigma_\beta^2} \qquad \text{and} \qquad h_f^2 = \frac{\sigma_\beta^2}{\frac{1}{k_3}\sigma_\varepsilon^2 + \frac{k_2}{k_3}\sigma_{\alpha_i\beta_j}^2 + \sigma_\beta^2}$$

All terms in the equations are as previously defined elsewhere. Notice that in computing individual-tree heritability for the field data, the effect of inbreeding that was considered in the greenhouse data was ignored. It was assumed that at 10 and 11 years inbreeding depression must have eliminated all inbred trees (see Mergen et al. 1965; Fowler and Park 1983; Park et al. 1984). Standard errors of heritability were computed as previously described (see section 3.3.2.1). The type B genetic correlations for studying the extent of genotype by environment interaction between site A and B were computed as described in Burdon (1977).

Expected genetic gain in 10- and 11-year height from direct mass selection on field height was estimated as in Falconer (1981):

$$\Delta G_f = i h_i^2 \sigma_P$$

where,

ΔG_f = Genetic gain or response to selection,

i = selection intensity if 5% of the test population is to be selected by truncation,

h_i^2 = narrow sense heritability expressed in the field,

σ_P = phenotypic standard deviation as expressed in the field.

ΔG_f was then expressed as the percentage of the population mean to obtain percentage genetic gain.

2.3.2.4 Efficiency of Early Selection

The ultimate objective of all preceding analyses was to find out how much gain or loss in 10- and 11-year height would be realised if selection were done based on greenhouse seedling results. Early selection is indirect selection performed on juvenile traits to improve the same or a different trait at advanced age. Computation of correlated gain involves the use of the genetic correlation coefficient between the two traits. In this study, the genetic correlation coefficients between field heights and all greenhouse-assessed traits were computed as described by Robertson (1959). With this method, the two traits whose correlation coefficient was to be estimated were converted to standard units. This involved subtracting the mean from each data point and dividing by standard deviation of the trait. The analysis of variance was then performed on a cross-site model with the field and greenhouse trials representing two contrasting sites as follows:

$$Y_{n(ij)} = \mu + \tau_i + \beta_j + \tau_i\beta_j + \varepsilon_{n(ij)}$$

where,

$Y_{n(ij)}$ = observation of n-th tree in the j-th family and i-th test site,

μ = general mean,

τ_i = effect due to i-th test site (field or greenhouse),

β_j = effect due to j-family,

$\tau_i\beta_j$ = family by site interaction,

$\varepsilon_{n(ij)}$ = error..

Let A = mean square for the family effect,

B = mean square for the family by site interaction effect

C = error mean square.

The genetic correlation between any two traits is then computed from the mean squares as follows:

$$r_{A_{gf}} = \frac{A - B}{A + B - 2C}$$

where $r_{A_{gf}}$ is the genetic correlation coefficient between the field and greenhouse trait. Standard errors of genetic correlation coefficients were computed according to Robertson (1959).

The correlated genetic gain in field height as the result of selection on greenhouse traits was estimated as described by Falconer (1981):

$$CG_f = i_f h_{i_g} h_{i_f} \sigma_{P_f} r_{A_{gf}}$$

where,

CG_f = correlated gain or response to selection in field height,

h_{i_g} and h_{i_f} = standard deviation of narrow sense heritability for greenhouse and field traits, respectively,

σ_{P_f} = phenotypic standard deviation for field height,

$r_{A_{gf}}$ = genetic correlation coefficient between greenhouse and field traits

i_f = selection intensity to be applied on field trait.

The CG_f was then expressed as the percentage of the population mean to obtain the percentage correlated gain. With the assumption that the same intensity of selection would be applied in the field and in the greenhouse, the efficiency of early selection was computed as described by Falconer (1981), as the ratio of correlated gain to gain from direct selection as expressed in the following equation:

$$E(\%) = \frac{CG_f}{\Delta G_f}.100 = \frac{h_{i_g} h_{i_f} \sigma_{P_f} r_{A_g}}{h_{i_f}^2 \sigma_{P_f}}.100 = \frac{h_{i_g} r_{A_g}}{h_{i_f}}.100$$

where E(%) is percentage gain efficiency due to indirect early selection. Other terms are as previously defined. For multiple trait selection, two types of selection indices were constructed as follows:

(1). Using more than one greenhouse traits to predict gain in field height. A three-trait selection index has the following form:

$$I_1 = b_2X_2 + b_3X_3 + b_4X_4$$

where, I_1 is a selection index for predicting expected gain in trait 1 as a result of selection for traits X_2, X_3 and X_4; b_2, b_3, and b_4 are coefficients or weights for traits X_2, X_3 and X_4, respectively. The normal equations for computing the coefficients for this selection index are described by Becker (1975) and Falconer (1981). They are as follows:

$$b_2P_{22} + b_3P_{23} + b_4P_{24} = A_{21}$$

$$b_2P_{32} + b_3P_{33} + b_4P_{34} = A_{31}$$

$$b_2P_{42} + b_3P_{43} + b_4P_{44} = A_{41}$$

where, P_s are phenotypic variances or covariances between the greenhouse traits and A_s are genetic covariances between greenhouse traits and field height.

(2). Combining field height with two greenhouse traits to predict expected genetic gain in field height. This index has the following form:

$$I_1 = b_1X_1 + b_2X_2 + b_3X_3$$

Normal equations for computing coefficients for this index are as follows:

$$b_1P_{11} + b_2P_{12} + b_3P_{13} = A_{11}$$

$$b_2P_{21} + b_2P_{22} + b_3P_{23} = A_{21}$$

$$b_3P_{31} + b_3P_{32} + b_3P_{33} = A_{31}$$

The second type of selection index is similar to the first one, except that the second one requires phenotypic and genetic variances for the field height, and phenotypic and genotypic covariances between greenhouse and field height. More discussion on selection indices is found in Chapter IV. The variances of the indices were computed as described in Falconer (1981):

$$\sigma_I^2 = b_2 A_{21} + b_3 A_{31} + b_4 A_{41} \qquad \text{and}$$

$$\sigma_I^2 = b_1 A_{11} + b_2 A_{21} + b_3 A_{31}$$

The correlation coefficient between index values and breeding values (r_{IA}) was computed also as described by Falconer (1981) using the following expression:

$$r_{IA} = \frac{\text{cov}_{IA}}{\sigma_I \sigma_A} = \frac{\sigma_I}{\sigma_A}$$

The correlation r_{IA} is then used to compute expected genetic gain due to index selection as follows:

$$R_I = i r_{IA} \sigma_A$$

where σ_A is the standard deviation of the additive genetic variance for the trait to be improved. Recall that expected gain from direct selection on field height is computed as $R_x = i h^2 \sigma_p$. All items in the equation are as described earlier. Assuming that the same selection intensity will be used in both index selection, and selection based on the trait to be improved alone, efficiency of index selection is computed as:

$$E = \frac{R_I}{R_x} = \frac{i r_{IA} \sigma_A}{i h^2 \sigma_p} = \frac{r_{IA} \sigma_A}{h^2 \sigma_p}$$

This formula produces exactly the same results as the one described by Wu et al. (2000) which is described here as follows:

$$E = \frac{\sigma_I \sigma_y}{\sigma_A^2}$$

where, σ_y is the phenotypic standard deviation of the trait to be improved.

In the first phase of analyses, greenhouse-field genetic correlations were computed with all 58 families. This produced very low genetic correlations for most of the traits. Ranking of family means for greenhouse TH36 against 11-year heights at site A (AH11) and site B (BH11) showed that there were large rank changes between greenhouse and field heights. Thus, a second phase of analyses was conducted excluding 15 families whose rank changes were considered too great to mask the correlation that might have existed in the larger subset of the data. The families that were excluded in this phase of analyses appear in Table 5 with their ranks in the greenhouse and the field. Each site was ranked separately against the greenhouse data. Thus, families excluded when computing correlations with site A were not exactly the same as those excluded when computing corelations with site B. However, the majority of the families excluded were the same for both sites. Genetic correlations, correlated gains and selection efficiencies will be presented when all 58 families are involved and when families in Table 5 are excluded. A detailed discussion about these families appears in Chapter IV.

Table 5: Family ranking for 36-week height in the greenhouse (TH36) and 11-week height in the field (AH11 or BH11) for families that were excluded from the second analysis of genetic correlations between greenhouse and field height

Greenhouse with Site A			Greenhouse with Site B		
Family	TH36	AH11	Family	TH36	BH11
1	48	1	1	49	16
3	3	58	2	1	42
5	40	4	5	41	8
7	6	38	8	5	48
8	4	26	10	57	5
10	56	13	16	48	11
13	9	36	17	32	2
15	51	16	20	2	55
20	2	49	28	6	40
21	7	29	31	29	4
27	8	56	49	12	43
28	5	50	50	53	19
50	52	9	51	21	1
52	41	8	52	42	6
53	27	5			

2.3.2.5 Symbols and Definitions of Traits

The following are symbols and definitions of all traits measured directly from the seedlings or derived from the original seedling traits. Symbols used to define field height are also included. These symbols will be used throughout the remaining part of the thesis and might also appear in the abstract.

1. FH2, FH4, FH6, FH8, FH10, FH12, FH14, FH16, FH18 –cumulative measurements of the first season height increment taken at two-week intervals starting from the second week after complete seed germination (FH2) to eighteenth week after germination (FH18). In these notations, **FH** stands for *first season height*

increment and the number that follow (2, 4, 6,…, 18) indicates the number of weeks after germination.

2. SH2, SH4, SH6, SH8, SH10, SH12, SH14, SH16, SH18 –cumulative measurements for the second season height increment taken at two-week intervals starting from the second week after budburst (SH2) to the eighteenth week after budburst (SH18). In these notations, **SH** stands for *second season height increment* and the number that follow (2, 4, 6,…, 18) indicates the number of weeks after budburst.
3. TH2, TH4, TH6, TH8, TH10, TH12, TH14, TH16, TH18, TH20, TH22, TH24, TH26, TH28, TH30, TH32, TH34, TH36 – cumulative measurements of seedling heights taken at two-week intervals from the second week (TH2) to the thirty-sixth week (TH36) after seed germination. The only difference between FH2 through FH18 (see No. 1) and TH2 through TH18 is that TH2 through TH18 exclude those seedlings whose heights were measured only in the first season (FH2 through FH18). Because of terminal dieback after over-wintering, second season (SH2 through SH28) height measurements for these seedlings were not available. Measurements of TH20 through TH36 include the first season's total height increment (TH18), i.e., total first season height only for those seedlings, which retained growth on the main leader for 36 weeks as follows:

   TH20=TH18+SH2, **TH22**=TH18+SH4, **TH24**=TH18+SH6, **TH26**=TH18+SH8, **TH28**=TH18+SH10, **TH30**=TH18+SH12, **TH32**=TH18+SH14, **H34**=TH18+SH16, **TH36**=TH18+SH18. Note that this operation automatically excludes seedlings in TH2 to TH18 whose second season height increments (SH) were unavailable.

In these notations, **TH** stands for *total seedling height* and the number that follow (2, 4, 6,…, 36) indicates the number of weeks after germination.

Analyses of data with TH2 through TH36 was meant to examine the age trend for the genetic variance, heritability and age-to-age correlations for height using only the data for seedlings whose growth on the main leader spanned 36 weeks.

4. k, r, $t_{0.5}$ - parameters of the logistic growth curves representing upper asymptotic height, maximum rate of growth and age at the point of inflection, respectively.
5. D24, D30, D36, D54, - root collar diameter at age 24, 30, 36, and 54 weeks, respectively.
6. BL - branch length.
7. NL - needle length.
8. NBR - number of branches.
9. NBD - number of buds.
10. TB2 - terminal budburst date at the start of the second season.
11. BB2 - budburst date on branches at the start of the second season.
12. SL - second season increment of selected branches for study of tissue components.
13. NSU - number of stem units or number of needles on SL.
14. MSUL - mean stem unit length (SL÷NSU = SL÷number of needles on SL).
15. FB -fresh weight for branches (needles included).
16. FS - fresh weight for main stem (needles included).
17. TFS - fresh weight for the whole shoot system (FB+FS).
18. DB - dry weight for branches (needles included).
19. DS - dry weight for the main stem (needles included).

20. TDS - dry weight for the whole shoot system (DB+DS).

21. DR - dry weight for the root system.

22. TBO - total biomass (BD+DS+DR).

23. HI - harvest index (DS÷TDS).

24. RSR - root-shoot dry weight ratio (DR÷TDS).

25. BI - branching index (DS÷DB).

26. ST - stem slender quotient (D36÷TH36).

27. CS - crown shape (BL÷TH36).

28. AH10, AH11 - 10 and 11-year height at field sites A, respectively.

29. BH10, BH11 - 10 and 11-year height at field site B, respectively.

Modifications or additional symbols applied on any of the symbols define in 1 through 29 are defined at the point where they occur.

CHAPTER III: RESULTS

3.1 Introductory Remarks

This chapter presents results for both the greenhouse and field phases of the study. The chapter is arranged such that results from the greenhouse appear first without making any reference to field trials. Results from the field trials appear next, and thereafter results from the two phases of the study are brought together when correlated gains and efficiencies of early selection are presented. As much as possible, results for similar or closely related traits appear under one subtitle. Dissimilar traits will appear together only in sections involving correlation coefficients between traits. Unless specified, family means for all traits are in Appendix 5.

3.2 Results from the Greenhouse Study

3.2.1 Height and Growth Curves

3.2.1.1 Variances and Heritability

At the end of the first season (FH18), the mean height of the tallest family was 160.6 mm and that of the shortest family was 80.6 mm (mean = 109.0 mm). Variation in the first season height was highly statistically significant, and accounted for approximately between 22.8% and 25.5% of the total variance (Table 6).

Table 6: Variance components and heritability estimates for cumulative biweekly height growth during the first growth season.

Trait	Percentage of Variance Components			Heritability Estimates	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
FH2	71.2	6.0***	22.8***	0.726±0.116	0.902±0.211
FH4	72.6	2.6***	24.8***	0.764±0.120	0.908±0.217
FH6	70.9	3.6***	25.5***	0.794±0.122	0.912±0.222
FH8	71.9	3.9***	24.2***	0.756±0.119	0.907±0.216
FH10	71.6	4.8***	23.6***	0.743±0.118	0.905±0.214
FH12	71.1	4.7***	24.2***	0.763±0.119	0.908±0.217
FH14	70.6	4.2***	25.2***	0.790±0.122	0.912±0.221
FH16	70.1	4.7***	25.3***	0.796±0.122	0.912±0.222
FH18	70.0	4.8***	25.2***	0.794±0.122	0.912±0.222

*** P = 0.001; σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

Individual-tree heritability for first season height was between approximately 0.73 and 0.80, whereas heritability of family means was approximately 0.91 (Table 6).

For the second season's height growth increment, the mean for the family with the highest total height growth increment (SH18) was 168.1mm and that of the family with the lowest height growth increment was 42.6 mm (mean = 94.7 mm). Table 7 shows the variances and heritability for the second season height increment.

Table 7: Variance components and heritability estimates for cumulative biweekly height growth during the second growth season.

Trait	Percentage of Variance Components			Heritability Estimates	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
SH2	88.2	6.4***	5.4***	0.173±0.032	0.500±0.086
SH4	88.0	6.5***	5.5***	0.178±0.033	0.507±0.087
SH6	84.2	8.0***	7.8***	0.255±0.046	0.603±0.102
SH8	84.5	6.0***	9.5***	0.302±0.053	0.646±0.111
SH10	84.5	5.4***	10.1***	0.322±0.056	0.662±0.115
SH12	84.9	5.0***	10.1***	0.318±0.055	0.660±0.114
SH14	85.8	4.8***	9.4***	0.297±0.052	0.642±0.110
SH16	85.7	4.8***	9.5***	0.299±0.052	0.644±0.111
SH18	86.1	5.0***	8.9***	0.299±0.053	0.644±0.111

*** P = 0.001; σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

Note that the second season height growth increment was less genetically variable than that in the first season, largely due to increase in the error and block variance components. Compared to the first season height growth increment, the error variance component for the second season height growth increment increased by approximately 14% (Table 7). Table 7 also shows that there were slight increases in the block variance, though not to the same extent as the error variance. As the result of increases in non-genetic components of the total variance, the family variance component accounted for only approximately 5% to 10% of the total variance. Consequently, the individual-tree

heritability was low, ranging from approximately 0.17 to 0.32. However, heritability for family means was high, ranging from 0.50 to 0.66 (Table 7)

Table 8 shows the range of family means for the three growth curve parameters predicted by the nonlinear regression.

Table 8: Means and range of family means for growth curve parameters for the two growth seasons.

Trait	First Growth Season			Second Growth Season		
	Mean	Min.	Max.	Mean	Min.	Max.
k (mm)	112.4	82.9	167.6	114.9	66.2	186.8
r (mm/day)	0.81	0.73	0.89	0.52	0.44	0.67
$t_{0.5}$ (days)	51.6	46.7	57.8	59.0	42.8	83.0

Min –minimum; Max. –maximum.

Considering the mean, the predicted upper asymptotic height (k) for the two seasons was approximately the same, though the range of family means was different. Table 8 also shows that seedlings had a higher rate of growth (r) during the first season than the second season, and reached the point of inflection ($t_{0.5}$) of their growth curve 7 days earlier than during the second season.

The percentages of the family variance component and heritability for k expressed in both seasons (Table 9) were almost the same as those of the corresponding total seasonal final observed heights, i.e., FH18 and SH18 (Table 6 and 7). Genetic variation

for the rate of growth was generally low, i.e., 7% and 4% of the total variance for the first and second season, respectively. This is also reflected in the low individual-tree heritability for *r* in both seasons (Table 9).

Table 9: Variance components and heritability estimates for the growth curve parameters for the first (above) and the second (below) growth seasons.

Trait	Percentage of Variance Component			Heritability Estimate	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
k	70.0	4.4***	25.7***	0.805±0.123	0.914±0.223
r	85.8	6.9***	7.2***	0.234±0.058	0.709±0.104
$t_{0.5}$	81.7	2.0***	16.4***	0.501±0.093	0.853±0.169
k	86.1	5.0***	8.92***	0.282±0.050	0.629±0.107
r	94.1	1.6*	4.3**	0.132±0.025	0.429±0.077
$t_{0.5}$	92.5	2.0*	5.5***	0.169±0.031	0.493±0.085

* P = 0.05; ** P = 0.01; * *** P = 0.001; σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

The percentage of the family variance component and individual-tree heritability for the time at the point of inflection ($t_{0.5}$) expressed during the second season was 1/3 of that expressed during the first season. During the second season, the error variance for $t_{0.5}$

increased by 10% compared to the first season, whereas variance due to replication (block) effect remained the same.

Table 10 presents the variance and heritability estimates computed from only the seedlings that maintained growth on the main leader to the end of the second growing season (TH2 to TH36). Seedlings that suffered terminal dieback during over-wintering that followed after the first growing season were not included in computing estimates in Table 10, since height growth on the main leader for such seedlings could not be assessed during the second growing season. The excluded seedlings represent approximately 18% of the original number of seedlings that were planted at the start of the experiment. Thus, variance component and heritability values for TH2 to TH18 may be close but not equal to those of FH2 to FH18 of the first season, since the two datasets were of slightly different sizes. This operation was meant to examine the age trend in the genetic variance and heritability for height from 2 weeks to 36 weeks after germination using only the seedlings that contributed to the variance throughout the 36-week study period.

Table 10 generally shows that, although the decline in the family variance was not uniform over time, it declined from values as high as 27% of the total variance in the early weeks of the experiment to 16.8% at the end of the second season. The individual-tree heritability declined in a manner similar to the genetic variance, from values as high as 0.86 in early weeks of the experiment to 0.53 at the end of the second season. Generally the heritability for family means showed little decline compared to the individual-tree heritability. It reached the highest value, approximately 0.90, in the early weeks of the experiment and the lowest value of 0.82 at the end of the second season.

Table 10: Variance components and heritability estimates for cumulative biweekly height growth studied over the period of 36 weeks after seed germination.

Trait	Percentage of Variance Components			Heritability Estimates	
	σ_e^2	σ_α^2	σ_β^2	h_i^2	h_f^2
TH2	71.0	5.8***	23.2***	0.740±0.122	0.874±0.191
TH4	71.2	2.5***	26.3***	0.810±0.128	0.887±0.200
TH6	70.0	3.2***	26.8***	0.830±0.129	0.890±0.202
TH8	72.5	3.5***	24.0***	0.747±0.123	0.876±0.192
TH10	72.5	4.9***	22.6***	0.712±0.120	0.869±0.187
TH12	67.9	5.9***	26.2***	0.836±0.130	0.891±0.203
TH14	67.5	5.5***	27.0***	0.858±0.131	0.895±0.205
TH16	71.5	5.0***	23.5***	0.741±0.122	0.874±0.191
TH18	71.3	5.2***	23.5***	0.742±0.123	0.875±0.191
TH20	71.6	5.9***	22.5***	0.717±0.120	0.870±0.188
TH22	72.3	5.9***	21.8***	0.696±0.119	0.865±0.185
TH24	72.4	6.0***	21.6***	0.689±0.118	0.864±0.184
TH26	73.6	5.5***	20.9***	0.663±0.116	0.858±0.180
TH28	74.8	5.3***	19.9***	0.631±0.113	0.850±0.175
TH30	76.2	5.1***	18.7***	0.592±0.109	0.839±0.169
TH32	77.8	5.0***	17.2***	0.544±0.104	0.824±0.161
TH34	77.9	5.2***	16.9***	0.533±0.102	0.821±0.160
TH36	78.0	5.2***	16.8***	0.532±0.102	0.821±0.159

*** P = 0.001; σ_e^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

3.2.1.2 Correlation Coefficients

Tables of correlation coefficients for this section are larger than those presented before in this chapter and most of them are in the landscape page format. Therefore, for easy placement of these tables in the thesis, they all appear at the end of the section. Age-to-age genetic, phenotypic and environmental correlation coefficients for height at two-week intervals were very high, as one would expect. To conserve space, these correlations are not presented in the thesis. Instead, only correlations between biweekly cumulative heights (TH2 through TH34) with the final height at the end of the second season (TH36) are presented (Table 11). These are correlations that are meaningful in showing the age trend in the correlation coefficient, since they relate every periodic height measurement to the final height. Table 11 shows that the genetic correlation between the 2-week height (TH2) and 36-week height (TH36) was generally low (r_A = 0.452). The genetic correlation increased consistently with the decrease in the age gap to 1.0 (TH34 and TH36).

Correlation coefficients between growth curve parameter k, r and $t_{0.5}$ with periodic height measurements from which they were computed are presented for all three methods that were used to fit the logistic growth function (see Chapter 2). This approach was taken after observing unusually high genetic correlations with corresponding low phenotypic and environmental correlations between r and periodic height measurements for the second growth season when all nine data points were used. As will be seen in the next paragraphs, presenting correlations from all three methods provided a framework for realistic interpretation of the relationship between height and its growth rate (r).

Table 12 shows the correlation coefficients between growth curve parameters and height for the first growth season. As an extrapolated height beyond the final height for the first season (FH18), k was highly correlated with first season cumulative biweekly height measurements and reached a genetic correlation of approximately 1.0 (k and FH18). The genetic correlation between height and the rate of growth (r) increased with age from almost 0 at the start of the season (consider the standard error) to around 0.5 in the middle of the season, then declined to a constant value depending on the method used. Initially, height showed a moderate negative genetic correlation with the time at the point of inflection ($t_{0.5}$). This correlation decreased in magnitude to almost 0 in the middle of the season and thereafter became increasingly positive, but generally remained on the very low side throughout the first season. Note that for the first season data, all three methods used to fit the logistic function to the data, produced almost the same correlation coefficients between k, r and $t_{0.5}$ with height (Table 12).

Table 13 shows the correlation coefficients between growth curve parameters and height during the second season. All three methods used to fit the logistic function showed that the genetic correlation between k and height was consistently high from the start to the end of the season. Table 13 also shows that the nonlinear regression and the method of sums of reciprocals, the two methods which used all nine data points, predicted high genetic correlations with corresponding low phenotypic and environmental correlations between r and height. To the contrary, the method of selected points that used only three selected intervals along the growth curve to fit the logistic function produced moderate to low genetic correlations, which bear a good resemblance with the corresponding phenotypic and environmental correlations. In addition,

correlations from the method of selected points were generally similar to those observed during the first season.

Considering the high standard errors, all three methods show that the genetic correlation between height and $t_{0.5}$ during the second season was very low and tended to increase with the age of seedlings. Although the genetic correlations between $t_{0.5}$ and height for the three methods are generally similar, the methods of selected points and sums of reciprocals have very similar correlations when standard errors of the genetic correlations for the two methods are considered. Phenotypic and environmental correlations showed the best similarity among the three methods (Table 13).

Table 14 shows the correlation coefficients between the growth curve parameters for the first and second growth seasons. During the first season, the genetic correlation between k and r was moderate and almost the same for all three methods. The genetic correlation between k and $t_{0.5}$ was low regardless of the method used. Except for the nonlinear regression method, where the genetic correlation between r and $t_{0.5}$ was very low and positive, the two parameters were slightly negatively correlated genetically. The phenotypic and environmental correlations between r and $t_{0.5}$ were negative regardless of the method used.

As mentioned earlier, the method of selected points described the genetic correlations involving second season growth curve parameters better than the other two methods. Thus, statements that follow refer to correlation results from the method of selected points. Table 14 shows that the genetic correlation between k and r during the second season was low, whereas the genetic correlation between k and $t_{0.5}$ was moderate. This is the reverse of the corresponding genetic correlations expressed during the first

season. In the second season, the negative genetic correlation between r and $t_{0.5}$ was stronger than that expressed in the first season.

Another factor that was considered in this study was whether or not the growth pattern that was expressed by families in the first season was maintained in the second season. In other words, are growth patterns stable over time? To answer this question, correlation coefficients were computed for growth curve parameters of the first season with those of the second season. These correlation coefficients appear in Table 15. Except for the genetic correlation for r, first and second growth season curve parameters were not correlated in any way. This is also reflected in the lack of correlation between the total height accumulated in the first season (FH18) and that accumulated in the second season (SH18). Table 15 also shows that correlations of growth curve parameters with TH36 varied from season to season except k. The correlations between TH36 with r and $t_{0.5}$ were generally low, considering the size of the standard errors.

Table 11: Correlation coefficients between cumulative biweekly height and cumulative 36-week height (TH36).

Trait 1	Trait 2	Correlation coefficient		
		r_A	r_P	r_E
TH36	TH2	0.452±0.100	0.240	0.185
	TH4	0.562±0.084	0.351	0.294
	TH6	0.630±0.074	0.402	0.340
	TH8	0.699±0.064	0.466	0.407
	TH10	0.744±0.057	0.521	0.464
	TH12	0.790±0.046	0.624	0.582
	TH14	0.833±0.037	0.687	0.652
	TH16	0.843±0.036	0.649	0.601
	TH18	0.843±0.036	0.651	0.603
	TH20	0.889±0.027	0.749	0.715
	TH22	0.910±0.022	0.778	0.747
	TH24	0.936±0.016	0.825	0.799
	TH26	0.970±0.001	0.988	0.985
	TH28	0.985±0.004	0.943	0.934
	TH30	0.994±0.001	0.978	0.975
	TH32	0.999±0.000	0.996	0.995
	TH34	1.000±0.000	1.000	1.000

r_A, r_P, r_E, -genetic, phenotypic, environmental correlations

Table 12: Genetic, phenotypic and environmental correlations for the first season logistic growth curve parameters and first season cumulative height computed by three different methods.

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
k	FH2	0.611±0.069	0.476	0.431	0.583±0.064	0.474	0.437	0.605±0.062	0.469	0.423
	FH4	0.789±0.041	0.711	0.683	0.772±0.040	0.698	0.672	0.787±0.037	0.708	0.680
	FH6	0.867±0.027	0.798	0.773	0.850±0.030	0.781	0.756	0.867±0.024	0.800	0.775
	FH8	0.929±0.015	0.881	0.864	0.915±0.016	0.856	0.837	0.930± 0.013	0.884	0.868
	FH10	0.968±0.007	0.935	0.924	0.958±0.008	0.912	0.897	0.968±0.006	0.935	0.924
	FH12	0.990±0.002	0.976	0.971	0.984±0.003	0.956	0.947	0.990±0.002	0.975	0.969
	FH14	0.999±0.000	0.995	0.994	0.997±0.001	0.984	0.979	0.999±0.000	0.993	0.991
	FH16	0.999±0.000	0.997	0.997	0.997±0.001	0.986	0.982	0.999±0.000	0.996	0.994
	FH18	0.999±0.000	0.997	0.997	0.997±0.001	0.986	0.982	0.999±0.000	0.997	0.996

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 12 Continues.

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
r	FH2	-0.127±0.139	-0.165	-0.176	0.073±0.173	-0.139	-0.177	0.058±0.108	-0.138	-0.177
	FH4	0.183±0.135	0.156	0.157	0.368±0.152	0.286	0.281	0.354±0.094	0.324	0.329
	FH6	0.360±0.106	0.361	0.376	0.514±0.130	0.484	0.497	0.478±0.083	0.485	0.502
	FH8	0.492± 0.106	0.502	0.522	0.592±0.114	0.589	0.607	0.557±0.074	0.558	0.575
	FH10	0.512±0.103	0.513	0.531	0.570±0.118	0.550	0.563	0.542±0.077	0.549	0.566
	FH12	0.497±0.105	0.459	0.470	0.527±0.127	0.478	0.485	0.501±0.081	0.459	0.466
	FH14	0.473±0.107	0.386	0.386	0.487±0.135	0.396	0.394	0.455±0.085	0.381	0.379
	FH16	0.471±0.107	0.376	0.374	0.484±0.135	0.390	0.388	0.452±0.085	0.372	0.369
	FH18	0.468±0.108	0.373	0.371	0.483±0.135	0.390	0.387	0.452±0.085	0.369	0.365

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 12 Continues.

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
$t_{0.5}$	FH2	-0.502±0.091	-0.318	-0.273	-0.505±0.096	-0.304	-0.259	-0.449±0.084	-0.342	-0.320
	FH4	-0.424±0.099	-0.403	-0.401	-0.409±0.108	-0.375	-0.371	-0.308±0.094	-0.287	-0.288
	FH6	-0.331±0.106	-0.383	-0.401	-0.319±0.118	-0.366	-0.383	-0.194±0.099	-0.237	-0.251
	FH8	-0.193±0.116	-0.277	-0.301	-0.186±0.125	-0.301	-0.332	-0.055±0.104	-0.156	-0.182
	FH10	-0.061±0.121	-0.146	-0.169	-0.060±0.129	-0.184	-0.215	0.062±0.104	-0.078	-0.113
	FH12	0.054±0.120	-0.006	-0.022	0.054±0.130	-0.053	-0.079	0.173±0.101	0.055	0.027
	FH14	0.141±0.117	0.108	0.100	0.144±0.128	0.066	0.047	0.262±0.096	0.162	0.139
	FH16	0.146±0.117	0.121	0.115	0.149±0.128	0.077	0.060	0.267±0.096	0.176	0.156
	FH18	0.141±0.117	0.122	0.118	0.145±0.128	0.077	0.062	0.262±0.096	0.180	0.162

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 13: Genetic, phenotypic and environmental correlations for the first season logistic growth curve parameters and second season cumulative height computed by three different methods.

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
k	SH2	0.868±0.056	0.616	0.598	0.884±0.031	0.533	0.499	0.919±0.016	0.604	0.572
	SH4	0.957±0.019	0.654	0.631	1.0040±0.001	0.441	0.393	0.955±0.008	0.619	0.588
	SH6	0.931±0.027	0.704	0.682	0.899±0.030	0.575	0.540	0.926±0.016	0.800	0.649
	SH8	0.942±0.022	0.795	0.779	0.912±0.028	0.657	0.627	0.941±0.014	0.749	0.771
	SH10	0.959±0.016	0.855	0.844	0.924±0.024	0.723	0.700	0.948±0.012	0.826	0.810
	SH12	0.971±0.011	0.920	0.914	0.944±0.018	0.798	0.782	0.962±0.009	0.889	0.880
	SH14	0.984±0.006	0.963	0.961	0.964±0.012	0.858	0.846	0.976±0.006	0.934	0.929
	SH16	0.993±0.003	0.982	0.981	0.977±0.007	0.884	0.874	0.987±0.003	0.951	0.955
	SH18	0.994±0.002	0.984	0.983	0.979±0.007	0.886	0.875	0.988±0.003	0.957	0.953

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 13 Continues.

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
r	SH2	0.903±0.052	0.072	0.027	0.688±0.124	0.114	0.088	0.420±0.141	-0.044	-0.041
	SH4	0.910±0.048	0.166	0.126	0.672±0.118	0.122	0.098	0.386±0.136	0.108	0.089
	SH6	0.896±0.050	0.299	0.261	0.768±0.106	0.285	0.258	0.539±0.137	0.288	0.213
	SH8	0.889± 0.051	0.411	0.379	0.764±0.115	0.324	0.300	0.512±0.149	0.297	0.274
	SH10	0.847±0.067	0.439	0.413	0.743±0.124	0.292	0.269	0.474±0.158	0.298	0.277
	SH12	0.790±0.090	0.424	0.401	0.705±0.138	0.230	0.204	0.434±0.163	0.236	0.216
	SH14	0.724±0.116	0.378	0.356	0.636±0.160	0.161	0.135	0.389±0.167	0.168	0.148
	SH16	0.685±0.123	0.345	0.323	0.589±0.175	0.127	0.101	0.347±0.173	0.130	0.110
	SH18	0.679±0.131	0.340	0.318	0.584±0.177	0.124	0.098	0.343±0.174	0.127	0.106

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 13 Continues.

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
$t_{0.5}$	SH2	-0.002±0.262	-0.200	-0.212	0.250±0.293	-0.089	-0.104	0.212±0.174	-0.137	-0.158
	SH4	0.099±0.257	-0.221	-0.241	0.380±0.245	-0.105	-0.124	0.287±0.156	-0.131	-0.047
	SH6	0.072±0.234	-0.216	-0.238	0.258±0.323	-0.128	-0.149	0.214±0.196	-0.158	-0.159
	SH8	0.115±0.222	-0.130	-0.151	0.293±0.336	-0.086	-0.108	0.256±0.200	-0.061	-0.084
	SH10	0.162±0.216	-0.050	-0.068	0.319±0.332	-0.017	-0.035	0.277±0.199	-0.002	-0.022
	SH12	0.226±0.211	0.067	0.054	0.375±0.315	0.082	0.068	0.325±0.191	0.108	0.094
	SH14	0.280±0.208	0.180	0.173	0.438±0.289	0.180	0.171	0.370±0.180	0.205	0.197
	SH16	0.337±0.200	0.251	0.245	0.498±0.269	0.232	0.224	0.422±0.171	0.267	0.260
	SH18	0.347±0.198	0.260	0.254	0.505±0.267	0.238	0.230	0.428±0.170	0.275	0.268

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 14: Genetic, phenotypic and environmental correlations between growth curve parameters for the first season (above) and the second season (below).

Trait 1	Trait 2	Nonlinear Regression			Sums of Reciprocals			Three Selected Points		
		r_A	r_P	r_E	r_A	r_P	r_E	r_A	r_P	r_E
k	*r*	0.443±0.111	0.327	0.321	0.433±0.144	0.278	0.261	0.430±0.087	0.322	0.313
	$t_{0.5}$	0.171±0.116	0.168	0.169	0.216±0.125	0.208	0.209	0.289±0.094	0.239	0.230
r	$t_{0.5}$	0.051±0.152	-0.328	-0.380	-0.183±0.093	-0.530	-0.575	-0.192±0.111	-0.403	-0.459
k	*r*	0.602±0.340	0.230	0.205	0.401±0.205	-0.101	-0.127	0.231±0.181	-0.049	-0.071
	$t_{0.5}$	0.442±0.381	0.394	0.392	0.666±0.183	0.573	0.578	0.554±0.141	0.487	0.489
r	$t_{0.5}$	-0.373±0.399	-0.321	-0.318	-0.471±0.164	-0.515	-0.520	-0.530±0.094	-0.527	-0.492

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 15: Between-season correlations of growth curve parameters (method of selected points) and their relationship to the 36-week total height growth.

Trait 1	Trait 2	Correlation Coefficient		
		r_A	r_P	r_E
FH18	SH18	0.098±0.147	0.050	0.041
k	k^+	0.082±0.147	0.052	0.046
r	r^+	0.469±0.132	0.013	-0.016
$t_{0.5}$	$t_{0.5}{}^+$	-0.040±0.169	0.011	0.014
k	TH36	0.666±0.080	0.507	0.472
k^+	TH36	0.787±0.059	0.846	0.858
r	TH36	0.521±0.116	0.216	0.177
r^+	TH36	0.249±0.153	0.118	0.088
$t_{0.5}$	TH36	-0.039±0.157	0.106	0.129
$t_{0.5}{}^+$	TH36	0.369±0.142	0.283	0.286

$^+$-Second-season traits; r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

As mentioned earlier, the first season data had a very good sigmoid curve compared to the second season data. Thus, observed and expected growth curves for the first season were plotted for all 58 families from the nonlinear regression method. These curves appear in Appendix 2. Ranking of families with respect to observed height and growth curve parameters for the first and second season appear in Appendix 3 and 4, respectively. Family means for TH36 appear together with all other traits studied in this thesis in Appendix 5.

3.2.2 Root Collar Diameter

Table 16 show variances and heritability estimates for the 24-, 30- 36- and 54-week root collar diameter. Generally root collar diameter was highly genetically variable and this genetic variability declined consistently with seedling age from 19.3% at the age 24 weeks to 7.1% at the age 54 weeks.

Table 16: Variance components and heritability estimates for root collar diameter

Trait	Percentage of Variance Component			Heritability Estimate	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
D24	79.7	6.0***	19.3***	0.620±0.090	0.869±0.184
D30	79.7	3.9***	16.4***	0.523±0.079	0.843±0.167
D36	81.9	3.7***	14.5***	0.456±0.071	0.820±0.153
D54	89.9	3.0**	7.1***	0.224±0.038	0.556±0.095

** P = 0.01, *** P = 0.001; σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

Note that variability in diameter among experimental blocks (replications) declined with seedling age, whereas the error variance increased with seedling age.

Age-to-age genetic correlations for root collar diameter were very high. Root collar diameter was also highly correlated genetically with stem height at all ages (Table 17). Attempts were made to establish relationships between root collar diameter and the growth curve parameter r and $t_{0.5}$ estimated for stem height. These correlation

coefficients appear in Table 18. As Table 18 shows, variation in r and $t_{0.5}$ did not have any relationship with variation in root collar diameter.

Table 17: Age-to-age correlations for diameter and correlation coefficients between diameter and stem height.

Trait 1	Trait 2	Correlation Coefficient		
		r_A	r_P	r_E
D24	D30	0.984±0.004	0.943	0.934
D24	D36	0.953±0.012	0.892	0.882
D30	D36	0.990±0.03	0.969	0.966
D24	TH18	0.763±0.052	0.664	0.636
D24	TH36	0.859±0.035	0.766	0.744
D30	TH18	0.729±0.060	0.601	0.571
D30	TH36	0.886±0.030	0.826	0.814
D36	TH18	0.687±0.070	0.547	0.518
D36	TH36	0.876±0.033	0.826	0.817

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively.

Table 18: Correlations between diameter and height growth curve parameters for the first (above) and second season (below).

Trait 1	Trait 2	Correlation Coefficient		
		r_A	r_P	r_E
D24	r	0.022±0.117	0.014	0.013
D30	r	0.025±0.120	-0.018	-0.024
D36	r	0.011±0.121	-0.035	-0.041
D30	$t_{0.5}$	-0.059±0.113	0.229	0.288
D36	$t_{0.5}$	-0.003±0.115	0.253	0.301
D24	r	NA	0.119	0.101
D30	r	NA	0.132	0.113
D36	r	NA	0.129	0.112
D24	$t_{0.5}$	-0.054±0.200	-0.076	-0.080
D30	$t_{0.5}$	-0.069±0.211	-0.076	-0.080
D36	$t_{0.5}$	-0.015±0.221	0.079	0.087

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively; NA –not available due to negative variance component,

3.2.3 Budburst, Branch and Needle Characteristics

Table 19 shows variances and heritability for budburst date, needle length, branch length, number of branches and number of buds on the main stem. The genetic variance and heritability for branch length were high and similar to those of 36-week stem height (Table 10). The number of branches (NBR) and number of buds (NBD) in the first season

section of the seedlings were also genetically variable and showed moderate individual-tree heritability and high heritability for family means.

Table 19: Variance components and heritability estimates for budburst, branch and needle characteristics.

Trait	Percentage of Variance Component			Heritability Estimate	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
BL	80.4	2.3***	17.3***	0.532±0.089	0.943±0.233
NBR	79.4	4.7***	15.9***	0.500±0.096	0.828±0.160
NBD	84.3	4.0***	11.7***	0.365±0.078	0.782±0.134
NL	76.5	2.2***	21.3***	0.653±0.111	0.882±0.194
TB2	81.5	3.5***	15.0***	0.468±0.091	0.833±0.158
BB2	81.8	3.6***	14.6***	0.451±0.099	0.826±0.155

*** P = 0.001; σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

Needle length (NL) showed high genetic variability with the family variance component accounting for approximately 21% of the total variance (Table 19). Like BL, NL showed less variability among replications. The genetic variance for budburst date of terminal buds (TB2) and buds on branches (BB2) both accounted for approximately (15% of the total variance. Values of individual-tree heritability for budburst dates were moderate, whereas the corresponding heritability values for family means were high (Table 19).

Genetic variation in growth rhythm traits such as the date for budburst and their relationship to growth traits, especially height, were given an extended coverage in

Chapter 1. Therefore, it was of interest in this study to determine the amount and nature of the relationship between the dates for budburst and stem height and root collar diameter. The correlation coefficients for the dates of budburst with stem height and diameter appear in Table 20.

Table 20: Correlation coefficients for the dates for budburst with stem height and diameter.

Trait 1	Trait 2	Correlation Coefficient		
		r_A	r_P	r_E
TH18	TB2	0.028±0.131	0.089	0.104
TH36	TB2	0.023±0.141	0.099	0.115
D24	TB2	0.230±0.129	0.205	0.200
D30	TB2	0.167±0.138	0.173	0.174
D36	TB2	0.127±0.143	0.160	0.166

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively

There was no relationship between height growth and the dates for budburst. Also when the standard errors of the genetic correlation coefficients are considered, it is clear that there was no meaningful relationship between root collar diameter and the dates for budburst.

3.2.4 Biomass Production

Table 21 presents the variances and heritability estimates for fresh and dry weight for various parts of the seedlings. Generally, both fresh and dry weights had low individual-

tree heritability and low to medium heritability for family means. In addition, heritability estimates for dry weight were not very different from those estimated from fresh weight.

Table 21: Variance components and heritability estimates for fresh and dry weight production.

Trait	Percentages of Variance Component			Heritability Estimate	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
FB	87.5	3.6*	8.9**	0.276±0.090	0.479±0.114
DB	88.7	1.3	10.0**	0.303±0.093	0.504±0.118
FS	89.0	6.4*	4.6*	0.147±0.078	0.318±0.094
DS	89.1	5.1*	5.8*	0.183±0.081	0.370±0.100
TFS	88.4	3.8*	7.8*	0.243±0.086	0.444±0.109
TDS	89.7	1.4	8.9**	0.264±0.089	0.472±0.113
TBO	89.5	1.9	8.6**	0.264±0.088	0.466±0.112
DR	88.8	3.4*	7.8*	0.224±0.083	0.444±0.109

* P = 0.05, * P = 0.01; σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

Correlation coefficients for fresh and dry weight of the same seedling part were very high (Table 22). Dry and fresh weights for branches were highly correlated with those of the main stem.

Table 22: Genetic, phenotypic and environmental correlations among biomass traits

Trait 1	Trait2	Correlation Coefficient		
		r_A	r_P	r_E
FB	FS	0.943±0.014	0.808	0.826
	DB	0.999±0.000	0.987	1.002
	DR	0.947±0.013	0.885	0.903
	RSR	0.252±0.117	0.486	0.471
FS	DS	1.015±0.004	0.976	0.978
	DR	0.962±0.010	0.850	0.855
	RSR	0.297±0.116	0.516	0.500
DB	DS	0.947±0.013	0.860	0.864
	DR	0.949±0.012	0.910	0.913
	RSR	0.269±0.115	0.508	0.485
DS	DR	0.955±0.011	0.879	0.883
	RSR	0.343±0.112	0.521	0.507
DR	RSR	0.582±0.083	0.739	0.725
TFS	TDS	1.001±0.000	0.991	0.992

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively

Pearson's correlation coefficients of family means for fresh and dry weights with height, diameter, branch length, needle length and tissue components appear in Table 23. These correlations show that fresh and dry weight for all seedling components were highly correlated with total seedling height, root collar diameter, and branch length.

Table 23: Pearson's correlation coefficients of family means for fresh and dry weights with growth-related traits of greenhouse seedlings

Seedling Part	Other growth-related greenhouse traits							
	TH36	D23	D3	BL	NL	NSU	MSUL	SL
FB	0.65***	0.76***	0.66***	0.77***	0.37*	0.60***	0.06	0.40**
DB	0.67***	0.77***	0.67***	0.79***	0.38*	0.59***	0.06	0.40**
FS	0.62***	0.76***	0.72***	0.75***	0.29*	0.50***	0.02	0.32*
DS	0.61***	0.73***	0.68***	0.72***	0.25	0.52***	0.01	0.31*
DR	0.58***	0.74***	0.67***	0.73***	0.28	0.53***	-0.03	0.29*
TFS	0.66***	0.79***	0.70***	0.79***	0.36*	0.59***	0.05	0.39**
TDS	0.67***	0.78***	0.68***	0.78***	0.34*	0.58***	0.05	0.39**

* P = 0.05, ** P = 0.01, *** P = 0.001

The correlations for fresh and dry weights with NSU were largely moderate, whereas the corresponding correlations for NL and the second season's branch increment (SL) were generally low. The correlations for fresh and dry weights with MSUL were approximately zero.

3.2.5 Tissue Components

Table 24 presents the variances and heritability estimates for tissue components that were studied from the second season section of the branches. Tissue components showed more variation among trees within the family than among families.

Table 24: Variance components and heritability estimates for branch tissue components for data in original units (above) and standard units (below).

Trait	Percentage of Variance Component			Heritablity Estimate	
	σ_ε^2	σ_γ^2	σ_β^2	h_i^2	h_f^2
SL	21.7	71.2***	7.1**	0.212±0.036	0.614±0.094
NSU	24.5	70.3***	5.2*	0.157±0.027	0.536±0.081
MSUL	26.4	64.1***	9.5***	0.286±0.047	0.688±0.110
SL	20.4	72.3***	7.3**	0.221±0.038	0.624±0.096
NSU	25.1	69.7***	5.2*	0.156±0.027	0.534±0.081
MSUL	25.1	64.8***	10.1***	0.304±0.050	0.702±0.115

* P = 0.05, ** P = 0.01, *** P = 0.001, σ_ε^2, σ_γ^2, σ_β^2, -error, branch-within-family, and family variance components, respectively; h_i^2, -individual-tree heritability; h_f^2 -heritability for family means.

The mean stem unit length (MSUL) was more genetically variable than the number of stem units (NSU). MSUL had less variation among trees within family than NSU. Individual-tree heritability estimates for NSU and MSUL were generally low, whereas the corresponding heritability estimates for family means were high. Note that standardisation did not change the amount and nature of variation contained in the data with original units; the genetic parameters from both datasets are almost the same.

The correlation coefficients between the stem tissue components appear in Table 25. Both NSU and MSUL were highly correlated genetically with the length of the stem (SL) from which they were assessed, though the genetic correlation between SL and MSUL was slightly higher than that of SL and NSU. Table 25 also shows that NSU and MSUL were genetically, phenotypically and environmentally independent.

Table 25: Genetic, phenotypic and environmental correlations among branch tissue components for data in original units (above) and standard units data (below).

Trait 1	Trait 2	Correlation Coefficient		
		r_A	r_P	r_E
SL	NSU	0.693±0.151	0.800	0.716
SL	MSUL	0.838±0.087	0.711	0.629
MSUL	NSU	0.183±0.285	0.172	-0.053
SL	NSU	0.712±0.203	0.812	0.748
SL	MSUL	0.828±0.130	0.712	0.604
MSUL	NSU	0.195±0.284	0.175	-0.066

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively

The relative degrees of determination of the stem length (SL) by NSU and MSUL from the analysis of path coefficients appear in Table 26. Note that SL was 58% determined by MSUL and 42% by NSU. Phenotypically and environmentally, NSU had more influence on SL than did MSUL.

Table 26: The relative degrees of determination of the branch length increment (SL) by the number of stem units and mean stem unit length derived from path. coefficient analysis

Trait	Genetic	Phenotypic	Environmental
NSU	0.42	0.58	0.60
MSUL	0.58	0.42	0.40

Although the tissue components were assessed from branches rather than the main stem, attempts were made to establish their relationship with total height of the main stem at the end of the first season (FH18), total height increment accumulated during the second season (SH18), and the overall height accumulated over the two seasons (TH36). These correlation coefficients appear in Table 27. Note that SL was highly correlated genetically with all three main stem traits, though the correlation was larger with SH18 and TH36 than with FH18. NSU was correlated genetically with SH18 and TH36 but not FH18. However, NSU was correlated phenotypically and environmentally with FH18, SH18 and TH36. Unlike NSU, MSUL was correlated genetically, phenotypically and environmentally with both FH18 and SH18. Considering the standard error of the genetic correlations, MSUL was slightly more correlated genetically with TH36 than did NSU.

Table 27: Correlation coefficient between tissue components with seasonal height of the main stem.

Trait	Trait 2	Correlation Coefficient		
		r_A	r_P	r_E
SL	FH18	0.575±0.161	0.519	0.539
	SH18	0.702±0.182	0.532	0.521
	TH36	0.772±0.126	0.626	0.621
NSU	FH18	0.170±0.324	0.378	0.430
	SH18	0.732±0.256	0.480	0.479
	TH36	0.660±0.296	0.534	0.550
MSUL	FH18	0.555±0.131	0.442	0.425
	SH18	0.455±0.219	0.351	0.337
	TH36	0.584±0.160	0.448	0.426

r_A, r_P, r_E, -genetic, phenotypic, and environmental correlation, respectively

Attempts were made to establish the relationship between tissue components assessed from branches and the growth rate (r) and time at the point of inflection ($t_{0.5}$) that were computed for the seasonal growth curves of the main stem. The genetic correlations were very low with high standard errors. All phenotypic and environmental correlation coefficients were less than 0.3. To conserve space, these correlation coefficients are not included in this thesis, as they do not yield any useful information to warrant their inclusion.

3.2.6 Seedling Architecture

In this section, seedling architecture represents all traits that are ratios of original seedling traits such as total height, diameter, branch length, and dry weights. The variances and heritability values for these seedling-part ratios appear in Table 28.

Table 28: Variance components and heritability estimates for seedling architectural traits

Trait	Percentage of variance Component			Heritability Estimate	
	σ_ε^2	σ_α^2	σ_β^2	h_i^2	h_f^2
ST	84.7	2.6**	12.7***	0.393±0086	0.762±0.139
CS	85.2	5.8***	9.0***	0.286±0.076	0.655±0.113
HI	72.5	21.4***	6.1**	0.233±0.106	0.433±0.108
RSR	82.8	9.0***	8.2***	0.271±0.089	0.474±0.113
BI	77.8	16.6***	5.6**	0.201±0.102	0.394±0.103

σ_ε^2, σ_α^2, σ_β^2, -error, block, and family variance components, respectively; h_i^2, - individual-tree heritability; h_f^2 -heritability for family means.

Note that ST, which is the ratio of root collar diameter at the end of the second season (D36) and the 36-week total height (TH36), had moderate individual tree heritability Individual tree heritability of all other architecture traits was generally low. Like ST, the ratio of the mean branch length (BL) to TH36 here referred to as *crown shape* (CS) had high heritability value for family means. The heritability of family means for all other seedling-part ratios was generally low or moderate similar to those observed for fresh or dry weights from which architecture traits were derived. The *harvest index* (HI) which is the ratio of main stem dry weight to total above ground dry weight and *branching index*

(BI) which is here expressed as the ratio of main stem dry weight to branch dry weight were almost equally genetically variable.

Table 29 shows Pearson's correlation coefficients of family means for seedling architecture traits with growth-related traits, namely height, diameter, branch length, needle length, and stem tissue components. Note that the harvest index (HI) and branching index (BI) were negatively correlated with all growth traits. The stem slender quotient (ST) and crown shape (CS) were negatively correlated with all traits except diameter, branch length, and NSU. Generally, NL was not significantly correlated with architecture traits except HI.

Table 29: Pearson's correlation coefficients between architecture traits and growth-related traits of greenhouse seedlings

Architecture Trait	Growth-related Greenhouse Traits							
	TH36	D23	D3	BL	NL	NSU	MSUL	SL
ST	-0.20	0.40**	0.41**	0.38**	-0.04	0.12	-0.28-*	-0.10
CS	-0.22	0.36**	0.36**	0.37**	-0.08	0.08	-0.30*	-0.13
HI	-0.40**	-0.41**	-0.32*	-0.45**	-0.29*	-0.43**	-0.18	-0.38**
RSR	0.11	0.38**	0.44**	0.34*	0.04	0.19	-0.25	0.16
BI	-0.40**	-0.41**	-0.31*	-0.44**	-0.27	-0.43**	-0.20	-0.40**

* P = 0.05, ** P = 0.01, *** P = 0.001

3.3 Results from Field Trials

The results from field trials cover variances, heritability, and genetic gains for height at 10 and 11 years for trees from the same maternal seedlots as the seed that were used for the greenhouse experiment. These variances and heritability estimates appear in Table 30. At site A, the between-family variance accounted for 5.6% of the total variance for height at ages 10 and 11 years. This variance was not statistically significant ($P > 0.05$). There was a very large family by block interaction that accounted for approximately 32% and 30% of the total variances at age 10 and 11 years, respectively. Individual-tree heritability and heritability for family means were generally low. It was estimated that by retaining 5% of the test population, approximately 15% gain in height could be made from mass selection. When families with extreme rank changes were excluded from the analysis to boost the genetic correlation between greenhouse traits and field height, the individual-tree heritability was reduced to approximately 0.180. This translates into a reduction in the expected gain to approximately 13.5%, assuming that 5% of the test population would be retained (Table 30).

At site B, the genetic variances and heritability were much lower than those expressed at site A. The family by block interaction was also large, accounting for approximately 20% of the total variance. Assuming that 5% of the test population would be retained, mass selection would yield approximately 4% and 3% increase (gain) in the population mean for age 10- and 11-year height, respectively. When families with extreme rank changes were excluded from the analysis the individual-tree heritability for the 11-year height was considerably reduced (Table 30).

Table 30: Percentages of variance components, heritability (standard errors below in bold font), and genetic gain from mass selection for 10- and 11-year field height when 5% of the test population is retained.

Trait	Variance Component[A]				Heritability Estimate[A]		Heritability Estimate[B]		Genetic Gain (%)	
	σ_ε^2	σ_α^2	$\sigma_{\alpha\beta}^2$	σ_β^2	h_i^2	h_f^2	h_i^2	h_f^2	ΔG^A	ΔG^B
AH10	59.2	3.1	32.1***	5.6	0.231	0.373	0.182	0.365	15.7	13.6
					0.075	**0.070**	**0.048**	**0.090**		
AH11	61.7	3.0	29.7***	5.6	0.231	0.383	0.178	0.363	15.3	13.5
					0.075	**0.070**	**0.047**	**0.088**		
BH10	77.8	1.2	19.4***	1.6	0.063	0.214	0.060	0.216	4.2	4.0
					0.035	**0.050**	**0.029**	**0.056**		
BH11	77.1	2.2	19.6***	1.1	0.044	0.157	0.026	0.107	2.8	1.7
					0.032	**0.045**	**0.027**	**0.046**		

*** P = 0.001, σ_ε^2, σ_α^2, $\sigma_{\alpha\beta}^2$, σ_β^2, -error, block, error by block, and family variance components, respectively; h_i^2 and h_f^2 -individual-tree and family means heritability, respectively; Superscripts A and B are estimates when all 58 families were included and when families with extreme rank changes were excluded, respectively.

3.4 Early Indirect Selection

3.4.1 Heritability for Reduced Datasets

As mentioned earlier, 15 families with extreme rank changes were excluded from the second phase of analyses at sites A and B to boost the greenhouse-field correlations, when analysis with all 58 families yielded very low genetic correlation coefficients. Reduction in the number of families from 58 to 43 caused some changes in the genetic variances and heritability estimates. For field data, heritability estimates with reduced datasets were presented in Table 30. For the greenhouse data, the new heritability estimates appear in Appendix 6. Despite the reduction in the number of families, heritability estimates for seasonal heights remained high. For example, when the number of families were reduced for analysis with field site A, heritability estimates for first season height remained almost the same as those computed from 58 families. For analysis with field site B, reduction of the number of families caused some reductions in the heritability estimates for first season height. For analysis with field site A, reduction in the number of families increased heritability for second season height increment compared to those estimated with 58 families. A similar operation for analysis with site B reduced heritability for second season height.

3.4.2 Greenhouse-field Genetic Correlations

The genetic correlations between greenhouse traits and field height computed with 58 families appear in Table 31. The best genetic correlations for height were those involving the first season greenhouse height (FH2 through FH18) and field height at site A (AH10 and AH11).

Table 31: Genetic correlations and their standard errors (bold) between greenhouse juvenile traits and field height growth at the age of 10 and 11 years on two test sites when all 58 families were involved in the analysis.

Field Traits	Greenhouse Traits															
	FH2	FH4	FH6	FH8	FH10	FH12	FH14	FH16	FH18	TH20	TH22	TH24	TH26	TH28	TH30	TH32	TH34
AH10	0.237	0.202	0.198	0.230	0.264	0.279	0.293	0.295	0.297	0.132	0.176	0.171	0.167	0.156	0.138	0.115	0.106
	0.154	**0.153**	**0.152**	**0.154**	**0.154**	**0.146**	**0.144**	**0.149**	**0.149**	**0.160**	**0.161**	**0.162**	**0.164**	**0.166**	**0.169**	**0.174**	**0.174**
AH11	0.260	0.225	0.220	0.243	0.271	0.279	0.288	0.289	0.291	0.132	0.142	0.132	0.122	0.110	0.090	0.067	0.156
	0.152	**0.152**	**0.151**	**0.154**	**0.153**	**0.146**	**0.144**	**0.150**	**0.150**	**0.162**	**0.163**	**0.164**	**0.166**	**0.168**	**0.171**	**0.175**	**0.175**
BH10	-0.096	-0.023	0.067	0.149	0.195	0.224	0.230	0.227	0.227	0.237	0.243	0.228	0.211	0.199	0.188	0.179	0.176
	0.212	**0.209**	**0.207**	**0.209**	**0.208**	**0.197**	**0.195**	**0.201**	**0.203**	**0.203**	**0.205**	**0.207**	**0.211**	**0.214**	**0.218**	**0.223**	**0.223**
BH11	-0.118	-0.047	0.043	0.119	0.163	0.192	0.202	0.199	0.200	0.211	0.216	0.203	0.189	0.177	0.167	0.158	0.155
	0.241	**0.238**	**0.237**	**0.240**	**0.240**	**0.228**	**0.225**	**0.234**	**0.235**	**0.235**	**0.237**	**0.238**	**0.242**	**0.246**	**0.251**	**0.256**	**0.257**

Table 31: Continues.

Field Traits	Greenhouse Traits															
	TH36	SH2	SH4	SH6	SH8	SH10	SH12	SH14	SH16	SH18	k	k^+	r	r^+	$t_{0.5}$	$t_{0.5}{}^+$
AH10	0.103	0.127	0.165	0.132	0.103	0.078	0.044	0.001	-0.016	-0.017	0.204	-0.074	0.089	0.311	0.216	-0.423
	0.174	**0.170**	**0.169**	**0.168**	**0.167**	**0.167**	**0.167**	**0.168**	**0.168**	**0.169**	**0.143**	**0.158**	**0.182**	**0.148**	**0.151**	**0.148**
AH11	0.055	0.076	0.087	0.055	0.031	0.011	-0.021	0.063	-0.078	-0.078	0.174	-0.126	0.061	0.339	0.160	-0.398
	0.176	**0.172**	**0.172**	**0.170**	**0.168**	**0.168**	**0.167**	**0.168**	**0.167**	**0.168**	**0.144**	**0.156**	**0.183**	**0.155**	**0.155**	**0.155**
BH10	0.173	0.055	0.126	0.022	-0.001	-0.010	-0.022	-0.040	-0.047	-0.049	0.244	-0.056	0.076	-0.071	0.413	-0.152
	0.224	**0.226**	**0.223**	**0.224**	**0.221**	**0.220**	**0.219**	**0.220**	**0.219**	**0.221**	**0.184**	**0.208**	**0.239**	**0.214**	**0.173**	**0.230**
BH11	0.150	0.040	0.109	0.000	-0.006	-0.013	-0.023	-0.044	-0.049	-0.053	0.219	-0.059	0.037	-0.055	0.424	-0.123
	0.257	**0.258**	**0.256**	**0.255**	**0.252**	**0.251**	**0.150**	**0.251**	**0.250**	**0.252**	**0.212**	**0.237**	**0.274**	**0.245**	**0.194**	**0.265**

Table 31: Continues.

Field Traits	Greenhouse Traits															
	D24	D30	D36	D54	BL	NL	NSU	MSUL	TB2	BB2	DB	FS	DS	TFS	TDS	DR
AH10	0.025	0.015	-0.036	-0.215	0.113	0.158	0.068	0.312	0.072	0.056	-0.124	-0.263	-0.309	-0.138	-0.178	-0.211
	0.153	**0.156**	**0.158**	**0.156**	**0.162**	**0.162**	**0.166**	**0.147**	**0.184**	**0.180**	**0.248**	**0.304**	**0.272**	**0.267**	**0.255**	**0.259**
AH11	-0.015	-0.032	-0.082	-0.265	0.080	0.105	0.039	0.302	0.107	0.100	-0.219	-0.375	-0.403	-0.242	-0.274	-0.290
	0.153	**0.156**	**0.158**	**0.152**	**0.163**	**0.164**	**0.167**	**0.148**	**0.183**	**0.179**	**0.240**	**0.281**	**0.252**	**0.256**	**0.243**	**0.248**
BH10	-0.121	-0.111	-0.111	-0.353	0.246	0.105	-0.197	0.599	0.060	0.079	-0.214	-0.298	-0.291	-0.195	-0.241	-0.222
	0.198	**0.202**	**0.205**	**0.187**	**0.202**	**0.215**	**0.210**	**0.137**	**0.241**	**0.235**	**0.315**	**0.390**	**0.360**	**0.343**	**0.324**	**0.338**
BH11	-0.115	-0.098	-0.098	-0.369	0.223	0.106	-0.241	0.526	0.080	0.101	-0.258	-0.404	-0.385	-0.259	-0.297	-0.246
	0.226	**0.230**	**0.235**	**0.211**	**0.234**	**0.245**	**0.235**	**0.176**	**0.274**	**0.267**	**0.352**	**0.409**	**0.382**	**0.379**	**0.358**	**0.381**

Table 31: Continues

Greenhouse Trait	Field Trait	Genetic Correlation	SE
ST	AH10	-0.237	0.178
	AH11	-0.225	0.179
	BH10	-0.401	0.207
	BH11	-0.356	0.245
CS	AH10	0.014	0.207
	AH11	0.014	0.207
	BH10	-0.192	0.261
	BH11	-0.134	0.304
HI	AH10	-0.171	0.265
	AH11	-0.189	0.263
	BH10	0.113	0.353
	BH11	0.075	0.405
RSR	AH10	-0.510	0.171
	AH11	-0.560	0.158
	BH10	-0.319	0.271
	BH11	-0.305	0.312
BI	AH10	-0.126	0.281
	AH11	-0.140	0.280
	BH10	0.230	0.354
	BH11	0.196	0.410

SE –standard error

These correlations reached a maximum of approximately 0.3 at age 10 and 0.29 at age 11 years. The corresponding correlations with field site B were much lower and often with high standard errors (Table 31). At site A, the correlations declined sharply at the start of the second season (TH20) and reached the lowest value of 0.103 at the 36-week height (TH36). Considering the size of the standard errors, the correlations between greenhouse height after the first season (TH20 through TH36) and field height at site B (BH10 and BH11) were generally zero. The second season height increment (SH2 through SH18) was not correlated genetically with field height at either site or ages (Table 31).

With all 58 families, the growth curve parameter r for the first season was not correlated with field height at both sites. The same parameter for the second season had a correlation with field height at site A of approximately 0.3 and 0.33 at age 10 and 11, respectively. It was not correlated with field height at site B. The first season $t_{0.5}$ was correlated with field height at site B ($r_A \approx 0.4$) but not at site A, whereas the second season $t_{0.5}$ was negatively correlated with field height at site A (Table 31).

The correlation between the mean stem unit length (MSUL) and field height at site A when all 58 families were involved was approximately 0.3. The correlation between MSUL and field height at site B was approximately 0.6 and 0.53 at age 10 and 11, respectively. It was noted that with all 58 families involved, all other traits not mentioned here were considered not correlated genetically with field height at either site or ages. These correlations are either equal or less than their standard errors (Table 31). Biomass and architecture traits were negatively correlated with field height (Table 31.

The greenhouse-field genetic correlations computed from 43 families by excluding 15 families with extreme rank changes at each site appear in Table 32. These

genetic correlations were computed in the second phase of analyses, by excluding 15 families whose rank changes for TH36 with AH11 and BH11 were considered too great to mask any meaningful correlation between field and greenhouse height that might have existed in a larger sub-set of the data. A careful examination of these correlations shows that a simple act of excluding 15 families whose greenhouse vs field rankings were extremely unstable for one trait achieved two important things that were lacking in the correlations involving all 58 families (Table 31) as follows:

1. It greatly improved the greenhouse-field genetic correlation coefficients for all traits and both test sites even for those traits that are not directly related to height. For example, correlations as high as 0.6 or slightly greater between greenhouse (TH2 to TH36) and field heights were observed at both sites. The second season height increments (SH2 to SH18) that were originally not correlated with field height are now correlated with it for both sites. Root collar diameter (D24 to D36), branch length (BL), needle length (NL) and the number of stem units (NSU) that were originally not correlated with field height are now correlated with it for a certain degree especially for site A.

2. Age-to-age trends in the genetic correlation coefficients were created that would normally be expected for a trait repeatedly measured at different ages. For example, there was a general trend for the correlation involving greenhouse height (TH2 to TH36) and field height to increase with age of the greenhouse seedlings. To a certain extent, a similar trend existed in the correlations involving the second season height increment (SH2 to SH18).

Table 32: Genetic correlations and their standard errors (bold) between greenhouse juvenile traits with field height growth at the age of 10 and 11 years on two test sites when 15 families with extreme rank changes were excluded from the analysis at each site.

Field Traits	Greenhouse Traits															
	FH2	FH4	FH6	FH8	FH10	FH12	FH14	FH16	FH18	TH20	TH22	TH24	TH26	TH28	TH30	TH32	TH34
AH10	0.224	0.308	0.367	0.468	0.517	0.545	0.555	0.553	0.553	0.564	0.584	0.592	0.595	0.581	0.577	0.571	0.574
	0.139	**0.133**	**0.126**	**0.115**	**0.108**	**0.103**	**0.101**	**0.101**	**0.101**	**0.101**	**0.098**	**0.097**	**0.097**	**0.100**	**0.102**	**0.104**	**0.104**
AH11	0.232	0.311	0.371	0.460	0.501	0.519	0.521	0.518	0.518	0.531	0.544	0.565	0.543	0.527	0.521	0.512	0.515
	0.139	**0.136**	**0.126**	**0.116**	**0.111**	**0.108**	**0.101**	**0.107**	**0.107**	**0.107**	**0.105**	**0.102**	**0.106**	**0.109**	**0.111**	**0.115**	**0.115**
BH10	0.136	0.218	0.280	0.354	0.393	0.442	0.463	0.463	0.462	0.501	0.526	0.546	0.588	0.612	0.634	0.626	0.632
	0.199	**0.193**	**0.184**	**0.176**	**0.170**	**0.163**	**0.159**	**0.159**	**0.158**	**0.154**	**0.150**	**0.147**	**0.139**	**0.135**	**0.131**	**0.135**	**0.133**
BH11	0.114	0.199	0.265	0.336	0.375	0.423	0.445	0.444	0.446	0.493	0.520	0.545	0.604	0.637	0.667	0.664	0.672
	0.293	**0.286**	**0.273**	**0.262**	**0.254**	**0.244**	**0.238**	**0.238**	**0.238**	**0.229**	**0.222**	**0.216**	**0.199**	**0.188**	**0.178**	**0.182**	**0.179**

Table 32: Continues

Field Traits	Greenhouse Traits															
	TH36	SH2	SH4	SH6	SH8	SH10	SH12	SH14	SH16	SH18	k	k^+	r	r^+	$t_{0.5}$	$t_{0.5}{}^+$
AH10	0.580	0.448	0.526	0.546	0.502	0.470	0.460	0.443	0.437	0.440	0.549	0.389	0.094	0.512	0.324	-0.300
	0.103	**0.140**	**0.131**	**0.118**	**0.122**	**0.127**	**0.130**	**0.135**	**0.137**	**0.137**	**0.101**	**0.148**	**0.167**	**0.160**	**0.139**	**0.212**
AH11	0.521	0.392	0.438	0.462	0.422	0.396	0.386	0.365	0.359	0.362	0.512	0.317	0.135	0.450	0.236	-0.297
	0.114	**0.149**	**0.147**	**0.133**	**0.134**	**0.138**	**0.141**	**0.147**	**0.148**	**0.149**	**0.107**	**0.158**	**0.166**	**0.174**	**0.148**	**0.214**
BH10	0.643	0.294	0.404	0.454	0.433	0.449	0.448	0.419	0.409	0.425	0.461	0.384	0.093	-0.075	0.382	0.247
	0.131	**0.237**	**0.227**	**0.210**	**0.210**	**0.206**	**0.206**	**0.213**	**0.213**	**0.213**	**0.159**	**0.214**	**0.223**	**0.374**	**0.186**	**0.299**
BH11	0.683	0.346	0.460	0.540	0.541	0.557	0.556	0.522	0.508	0.526	0.445	0.464	0.083	0.049	0.400	0.321
	0.174	**0.335**	**0.314**	**0.275**	**0.268**	**0.261**	**0.261**	**0.276**	**0.279**	**0.275**	**0.238**	**0.288**	**0.328**	**0.551**	**0.269**	**0.420**

Table 32: Continues

Field Traits	Greenhouse Traits															
	D24	D30	D36	D54	BL	NL	NSU	MSUL	TB2	BB2	DB	FS	DS	TFS	TDS	DR
AH10	0.388	0.353	0.294	0.046	0.402	0.302	0.453	0.540	0.137	0.042	0.361	0.354	0.284	0.420	0.354	0.137
	0.130	**0.137**	**0.146**	**0.186**	**0.128**	**0.137**	**0.188**	**0.120**	**0.161**	**0.163**	**0.190**	**0.409**	**0.403**	**0.214**	**0.217**	**0.213**
AH11	0.333	0.285	0.225	-0.022	0.356	0.238	0.387	0.541	0.171	0.089	0.249	0.217	0.162	0.290	0.237	0.060
	0.137	**0.145**	**0.152**	**0.187**	**0.134**	**0.143**	**0.202**	**0.120**	**0.160**	**0.163**	**0.206**	**0.448**	**0.429**	**0.239**	**0.235**	**0.218**
BH10	0.146	0.134	0.125	-0.119	0.370	0.326	0.071	0.714	0.158	0.129	-0.070	-0.382	-0.363	-0.016	-0.137	-0.291
	0.212	**0.218**	**0.222**	**0.274**	**0.182**	**0.188**	**0.329**	**0.112**	**0.204**	**0.206**	**0.423**	**0.710**	**0.623**	**0.513**	**0.471**	**0.353**
BH11	0.193	0.195	0.196	-0.073	0.352	0.324	0.141	0.623	0.197	0.168	0.039	-0.453	-0.373	0.117	-0.035	-0.199
	0.306	**0.313**	**0.318**	**0.406**	**0.272**	**0.277**	**0.475**	**0.206**	**0.295**	**0.298**	**0.623**	**0.969**	**0.906**	**0.743**	**0.703**	**0.543**

3.4.3 Correlated Genetic Gains

Correlated genetic gains also called correlated responses to selection, that were computed with all 58 families and those computed with 43 families appear together in Table 33. These gains are presented as percentages of the population mean, assuming that 5% of the population would be retained under truncated mass selection. It should be clearly understood at this point that the absolute correlated genetic gains provided in Table 33 cast a true picture of what early selection could achieve especially for field site B. As will be seen in the next section when efficiencies of early selection are presented, correlated gains for site B were more realistic when looked at in terms of absolute rather than relative gains. i.e., gain efficiencies.

The correlated genetic gains computed from the 43 families were much larger than those computed from the 58 families. Much larger correlated gains could be obtained by selection based on absolute height in the greenhouse to improve field height at site A rather than site B. All negative genetic gains in Table 33 imply that the population mean would be reduced by an indicated percentage if selection was based on that trait.

Table 33: Correlated genetic gain in 10- and 11-year height at site A and B due to selection on juvenile greenhouse traits, estimated from all 58 families (regular font) and from a subset of 43 families (bold font), when 5% of the test population is retained.

Field Traits	Greenhouse Traits																
	FH2	FH4	FH6	FH8	FH10	FH12	FH14	FH16	FH18	TH20	TH22	TH24	TH26	TH28	TH30	TH32	TH34
AH10	6.7	6.0	5.9	6.5	7.3	8.3	8.9	8.3	8.4	4.5	4.8	4.6	4.4	4.1	3.5	2.8	2.5
	6.2	**8.4**	**10.2**	**12.7**	**14.0**	**14.9**	**15.5**	**15.5**	**15.5**	**15.0**	**15.4**	**15.5**	**15.3**	**14.8**	**14.2**	**13.4**	**13.2**
AH11	7.1	6.4	6.4	6.7	7.3	8.1	8.5	7.9	8.0	3.6	3.8	3.4	3.2	2.9	2.2	1.6	1.3
	6.4	**8.5**	**10.4**	**12.6**	**13.7**	**14.2**	**14.6**	**14.6**	**14.7**	**14.3**	**14.5**	**14.9**	**14.1**	**13.5**	**12.9**	**12.1**	**11.9**
BH10	-1.4	-0.3	1.0	2.1	2.7	3.4	3.5	3.3	3.3	3.3	3.4	3.2	2.9	2.6	2.4	2.2	2.1
	1.8	**2.9**	**3.9**	**4.8**	**5.3**	**5.9**	**6.2**	**6.2**	**6.2**	**6.4**	**6.5**	**6.5**	**6.6**	**6.6**	**6.5**	**6.2**	**6.1**
BH11	-1.4	-0.6	0.5	1.4	1.9	2.4	2.5	2.3	2.3	2.4	2.4	2.3	2.1	1.9	1.7	1.6	1.5
	1.0	**1.7**	**2.3**	**2.9**	**3.2**	**3.6**	**3.8**	**3.8**	**3.8**	**4.0**	**4.1**	**4.2**	**4.3**	**4.3**	**4.4**	**4.2**	**4.2**

Table 33: Continues.

Field Traits	Greenhouse Traits															
	TH36	SH2	SH4	SH6	SH8	SH10	SH12	SH14	SH16	SH18	k	k^+	r	r^+	$t_{0.5}$	$t_{0.5}{}^+$
AH10	2.5	1.7	2.3	2.2	1.8	1.4	0.8	0.0	-0.3	-0.3	6.0	-1.4	-1.4	3.5	4.8	-4.4
	13.3	**7.5**	**8.1**	**10.1**	**10.1**	**9.5**	**9.0**	**8.1**	**7.9**	**7.9**	**15.7**	**6.5**	**1.5**	**5.9**	**7.2**	**-3.1**
AH11	1.3	1.0	1.2	0.9	0.5	0.2	-0.4	-1.1	-1.4	-1.4	5.0	-2.5	-0.9	2.6	3.4	-4.0
	12.0	**6.6**	**6.8**	**8.6**	**8.5**	**8.1**	**7.6**	**6.7**	**6.5**	**6.5**	**14.7**	**5.3**	**2.1**	**5.2**	**5.3**	**-3.1**
BH10	2.1	0.4	0.9	0.2	-0.0	-0.1	-0.2	-0.4	-0.4	-0.4	3.6	-0.5	0.6	-0.4	4.6	-0.8
	6.2	**2.1**	**2.6**	**3.1**	**3.1**	**3.2**	**3.2**	**3.0**	**3.0**	**3.0**	**6.1**	**2.9**	**0.8**	**-0.3**	**3.8**	**1.3**
BH11	1.5	0.2	0.6	0.1	-0.0	-0.1	-0.2	-0.3	-0.4	-0.4	2.6	-0.4	0.2	-0.3	3.8	-0.5
	4.2	**1.6**	**1.9**	**2.3**	**2.5**	**2.5**	**2.5**	**2.4**	**2.3**	**2.4**	**3.8**	**2.2**	**0.5**	**0.1**	**2.5**	**1.1**

Table 33: Continues.

Field Traits	Greenhouse Traits															
	D24	D30	D36	D54	BL	NL	NSU	MSUL	TB2	BB2	DB	FS	DS	TFS	TDS	DR
AH10	0.6	0.4	-0.8	-3.3	2.7	4.2	0.9	5.5	1.6	1.2	-2.2	-3.3	-4.3	-2.2	-3.0	-3.4
	9.2	**7.7**	**6.0**	**0.7**	**9.5**	**7.5**	**6.1**	**11.7**	**2.4**	**0.8**	**5.5**	**2.4**	**2.0**	**5.2**	**4.6**	**2.1**
AH11	-0.4	-0.7	-1.8	-4.0	1.9	2.7	0.5	5.1	2.3	2.1	-3.8	-4.6	-5.5	-3.8	-4.5	-4.6
	7.9	**6.3**	**4.6**	**-0.3**	**8.5**	**6.0**	**5.3**	**11.8**	**3.1**	**1.6**	**3.8**	**1.5**	**1.2**	**3.6**	**3.1**	**0.9**
BH10	-1.6	-1.3	-1.2	-2.8	3.0	1.4	-1.3	5.3	0.7	0.9	-2.0	-1.9	-2.1	-1.6	-2.1	-1.8
	1.5	**1.3**	**1.1**	**-0.8**	**4.1**	**3.8**	**0.5**	**8.0**	**1.9**	**1.5**	**-0.4**	**-1.0**	**-1.7**	**-0.01**	**-0.6**	**-1.7**
BH11	-1.2	-1.0	-0.9	-2.4	2.2	1.2	-1.3	3.8	0.7	0.9	-1.9	-2.1	-2.2	-1.7	-2.1	-1.6
	1.3	**1.1**	**1.2**	**-0.3**	**2.5**	**2.4**	**0.6**	**4.5**	**1.5**	**1.3**	**0.1**	**-0.8**	**-0.7**	**-0.3**	**-0.1**	**-0.7**

Table 33: Continues

Greenhouse Trait	Field Trait	Correlated Gain
ST	AH10	-4.8
	AH11	-5.2
	BH10	-5.6
	BH11	-5.3
CS	AH10	0.2
	AH11	0.3
	BH10	-2.3
	BH11	-1.7
HI	AH10	-2.7
	AH11	-3.4
	BH10	1.2
	BH11	0.8
RSR	AH10	-8.7
	AH11	-10.8
	BH10	-3.7
	BH11	-3.7
BI	AH10	-1.8
	AH11	-2.3
	BH10	2.3
	BH11	2.1

3.4.4 Efficiency of Early Selection

Efficiency of indirect selection including early selection is the genetic gain from indirect selection (selection applied on a different trait) expressed as the percentage of the genetic gain from direct selection (selection applied on the trait of interest). As mentioned earlier, field site B had very low heritability and consequently low genetic gain from direct selection. On the other hand, young greenhouse traits, especially height, had high heritability and therefore high correlated gain relative to gain from direct selection at site B. This combination of events led to unreasonably high efficiencies of early selection for height at site B (Table 34). Efficiencies of early selection for site B are probably unrealistic. Instead, the benefits from early selection can be better discussed by examining efficiencies of early selection for site A only. Therefore, in presenting and discussing efficiencies of early selection, greater emphasis will be given to site A than site B.

Table 34 presents efficiencies of early selection expressed as percentages of gain from direct selection. With all 58 families involved, the highest efficiency obtained was 56.5% (FH14). In general the best greenhouse predictor of field height was the first season height (FH2 to FH18) and first season growth curve parameter *k*. The MSUL had selection efficiency of 34.7% and 33.6% at 10 and 11 years, respectively. All other traits had much lower gain efficiencies.

Table 34 shows that with 43 families, early selection could be very efficient over direct selection on field height. Cumulative two-season heights (TH2 to TH36) had selection efficiencies in the range of 45.3% and 114.3%, whereas the second season

height increments (SH2 to SH18) had selection efficiencies in the range of 54.9% to 74.5%.

Table 34: Selection efficiencies (%) for 10- and 11-year height at site A and B due to selection on greenhouse juvenile traits, estimated from all 58 families (regular font) and from a subset of 43 families (bold font), assuming that the same selection intensity is applied on both greenhouse and filed traits.

Field Traits	Greenhouse Traits															
	FH2	FH4	FH6	FH8	FH10	FH12	FH14	FH16	FH18	TH20	TH22	TH24	TH26	TH28	TH30	TH32	TH34
AH10	42.5	37.9	37.5	41.3	46.3	53.1	56.5	52.8	53.5	28.4	30.6	29.5	28.2	25.9	22.1	17.1	16.1
	45.3	**61.6**	**75.3**	**93.6**	**103.0**	**109.2**	**114.0**	**114.2**	**114.3**	**110.6**	**113.6**	**114.2**	**112.8**	**108.6**	**104.4**	**98.5**	**96.9**
AH11	46.6	42.1	41.7	43.7	47.5	53.0	55.5	51.7	52.2	23.3	24.6	22.7	20.7	18.2	14.4	10.2	8.6
	47.4	**62.9**	**77.0**	**93.3**	**101.0**	**105.1**	**108.2**	**108.3**	**108.4**	**105.3**	**107.0**	**110.4**	**104.3**	**99.8**	**95.4**	**89.3**	**87.9**
BH10	-32.7	-8.2	24.3	51.0	65.2	81.3	84.4	77.7	77.7	79.8	80.4	75.3	68.3	62.8	57.5	52.4	51.1
	45.7	**73.1**	**97.4**	**121.4**	**134.5**	**148.8**	**155.9**	**156.1**	**156.3**	**161.1**	**164.4**	**165.7**	**167.5**	**165.8**	**163.6**	**155.6**	**155.3**
BH11	-48.3	-20.1	18.7	49.2	65.4	83.9	89.6	81.8	82.2	85.0	85.9	80.4	73.4	67.1	61.4	55.4	53.9
	58.7	**101.5**	**140.5**	**175.4**	**195.1**	**216.9**	**228.4**	**228.4**	**229.6**	**241.6**	**247.6**	**252.0**	**262.1**	**262.9**	**262.5**	**251.5**	**251.4**

Table 34: Continues.

Field Traits	Greenhouse Traits															
	TH36	SH2	SH4	SH6	SH8	SH10	SH12	SH14	SH16	SH18	k	k^+	r	r^+	$t_{0.5}$	$t_{0.5}{}^+$
AH10	15.7	11.0	14.5	13.9	11.7	9.2	5.1	0.1	-1.8	-1.9	37.9	-8.7	-9.1	22.4	30.2	-27.9
	97.6	**54.9**	**59.6**	**74.5**	**74.0**	**70.1**	**66.3**	**59.6**	**57.8**	**57.8**	**115.4**	**47.8**	**10.9**	**43.4**	**53.2**	**-23.0**
AH11	8.4	6.5	7.7	5.8	3.6	1.3	-2.5	-7.1	-8.9	-8.9	32.4	-14.8	-6.2	17.2	22.3	-26.2
	88.7	**48.8**	**50.2**	**63.8**	**63.1**	**59.7**	**56.3**	**49.6**	**48.1**	**48.1**	**108.9**	**39.4**	**15.9**	**38.5**	**39.1**	**-23.1**
BH10	50.0	9.0	21.1	4.4	-1.2	-2.2	-4.9	-8.7	-10.3	-10.7	86.6	-12.6	14.8	-9.7	110.1	-19.1
	156.8	**52.5**	**66.6**	**78.1**	**77.6**	**81.0**	**81.0**	**75.1**	**74.7**	**75.8**	**155.3**	**73.4**	**20.2**	**-8.3**	**95.9**	**33.0**
BH11	52.2	8.0	21.8	2.5	-1.6	-3.6	-6.3	-11.4	-12.8	-13.8	93.2	-15.9	8.7	-9.2	135.5	-18.5
	253.6	**94.1**	**115.5**	**141.5**	**147.7**	**153.2**	**153.3**	**142.6**	**141.4**	**142.9**	**228.2**	**135.2**	**27.6**	**8.3**	**152.9**	**65.4**

Table 34: Continues.

Field Traits	Greenhouse Traits															
	D24	D30	D36	D54	BL	NL	NSU	MSUL	TB2	BB2	DB	FS	DS	TFS	TDS	DR
AH10	4.1	2.3	-5.1	-21.2	17.1	26.6	5.6	34.7	10.2	7.9	-14.2	-20.9	-27.5	-14.1	-19.2	-21.7
	67.3	**56.8**	**43.9**	**5.1**	**70.0**	**55.4**	**45.2**	**86.4**	**17.9**	**5.6**	**40.1**	**17.6**	**15.0**	**38.3**	**34.0**	**15.4**
AH11	-2.4	-4.8	-11.5	-26.1	12.2	17.6	3.2	33.6	15.3	13.9	-25.1	-29.9	-35.9	-24.9	-29.6	-29.8
	58.5	**46.4**	**34.0**	**-2.5**	**62.6**	**44.2**	**39.0**	**87.6**	**22.6**	**12.0**	**28.0**	**10.9**	**8.7**	**26.7**	**23.0**	**6.8**
BH10	-37.8	-31.9	-29.9	-66.5	71.3	33.56	-31.1	127.3	16.4	21.2	-46.7	-45.4	-49.4	-38.2	-49.6	-43.5
	38.1	**31.9**	**27.8**	**-19.9**	**104.1**	**94.9**	**11.9**	**201.6**	**47.2**	**38.7**	**-9.2**	**-25.7**	**-28.3**	**-1.7**	**-16.0**	**-42.6**
BH11	-43.3	-33.7	-31.1	-88.5	77.6	40.7	-45.5	134.0	26.1	32.3	-67.7	-73.8	-78.4	-60.9	-73.5	-58.0
	76.7	**70.7**	**66.3**	**-18.6**	**151.0**	**143.9**	**36.1**	**268.1**	**89.6**	**76.7**	**7.9**	**-46.4**	**-44.2**	**19.3**	**-6.2**	**-44.4**

Table 34: Continues

Greenhouse Trait	Field Trait	Selection Efficiency
ST	AH10	-30.9
	AH11	-29.3
	BH10	-99.8
	BH11	-106.5
CS	AH10	1.5
	AH11	1.5
	BH10	-40.9
	BH11	-34.2
HI	AH10	-17.1
	AH11	-19.0
	BH10	21.6
	BH11	17.2
RSR	AH10	-55.3
	AH11	-60.6
	BH10	-65.9
	BH11	-75.7
BI	AH10	-11.7
	AH11	-13.1
	BH10	40.9
	BH11	41.8

Other traits with reasonably high efficiencies of early selection included k for first and second season, first season r and second season $t_{0.5}$, D24, D30, D36, BL, NL, NSU, and MSUL.

3.5 Multiple Trait Selection Efficiencies

This section presents two types of gain efficiencies from multiple trait selection namely:
(1) combining three greenhouse traits to indirectly predict gain in 11-year height relative to the gain expected from direct selection on 11-year height at site A (AH11) and,
(2) combining 11-year height with two greenhouse traits to increase gain in field height relative to the gain expected from selection based on 11-year height (AH11) alone.

Results from these two types of multiple trait selection indices appear in Table 35. The first eight entrees in Table 35 represent a combination of 11-year height at site A and two traits from the greenhouse retrospective study. Note that combining information on AH11 with information from siblings raised in the greenhouse for one growing season would increase genetic gain in 11-year height by between 1% and 8%. Table 35 also shows that the highest increases in genetic gain are those combining height at the end of the first growth season (FH18) and mean stem unit length (MSUL). An index combining AH11 with FH18 and the maximum rate of height growth during the first season (R_1) produced the same expected gain as the index involving AH11, FH18 and the date for the terminal budburst at the beginning of the second growth season (TB2). Combining AH11 with TB2 and R_1 would produce the least gain (1%) compared to selection based on information on AH11 alone. Analysis of first season growth curve showed that FH18 and the upper asymptotic height during the first season (K_1) were highly correlated

genetically (r_A = 0.999). Thus, FH18 can be replaced with K_1 without changing the expected gain from index selection (Table 35).

The last three indices in Table 35 are those combining only greenhouse traits to predict field height. Note that most of the greenhouse traits, especially those assessed in the second and third growth seasons had very low or negative genetic correlation with field height. Thus, although many growth-related greenhouse traits had favourable genetic correlations with each other, they were not good for inclusion in selection indices designed to predict gain in field height because of their poor genetic correlation with field height. In addition, some traits had low positive genetic correlations and negative phenotypic covariances with field height leading to negative weights for these traits. Thus, only three indices are presented for the selection index category involving greenhouse traits only. It is clear that, except for the selection index involving MSUL, combining greenhouse traits without considering information on field height itself would in this study capture very little of the gain expected from direct selection on AH11.

Table 35: Selection efficiencies from multiple trait selection indices at site A.

Trait combination	Coefficients (weights)				r_{IA}	E	%
	b_1	b_2	b_3	b_4			
$(AH11)b_1+(FH18)b_2+(R_1)b_3$	0.0958	0.3266	12.3477		0.321	1.039	4
$(AH11)b_1+(FH18)b_2+(MSUL)b_3$	0.1203	0.5964	41.6934		0.376	1.080	8
$(AH11)b_1+(FH18)b_2+(TB2)b_3$	0.0958	0.3362	0.7584		0.321	1.039	4
$(AH11)b_1+(MSUL)b_2+(TB2)b_3$	0.1215	160.9063	3.5414		0.362	1.039	4
$(AH11)b_1+(MSUL)b_2+(R_1)b_3$	0.1181	145.8174	149.6417		0.372	1.069	7
$(AH11)b_1+(R_1)b_2+(TB2)b_3$	0.0954	45.6625	1.1219		0.313	1.010	1
$(AH11)b_1+(FH18)b_2+(T_{0.51})b_3$	0.0961	0.3078	19.6877		0.327	1.057	6
$(AH11)b_1+(K_1)b_2+(T_{0.51})b_3$	0.0962	0.3020	18.3503		0.327	1.057	6
$(FH18)b_2+(R_1)b_3+(T_{0.51})b_4$		0.2205	60.8599	24.3052	0.112	0.361	
$(FH18)b_2+(R_1)b_3+(TB2)b_4$		0.3021	22.5485	0.9821	0.089	0.286	
$(R_1)b_2+(T_{0.51})b_3+(MSUL)b_4$		244.3193	31.4865	77.1003	0.201	0.650	

r_{IA} –correlation between index and breeding values, E –selection efficiency

3.6 Genotype-Environment Interaction

The genetic correlations between the two field test-sites showed that height exhibited high genotype by environment interaction (GE) due to changes in ranking of families at the two sites (Table 36). Type B genetic correlations were greater than 1.0, whereas both Pearson's and Spearman's rank correlations for family means ranged from approximately 0.36 to 0.4. The correlations for family means were higher at age 11 than at age 10 years.

Table 36: Genetic correlations and family-mean correlations for 10- and 11-year heights between field site A and B.

Site A	Site B	r_A	r_P	r_S
AH10	BH10	1.523	0.378**	0.361**
AH11	BH11	1.322	0.404**	0.393**

** P = 0.01; r_A; type B genetic correlation; r_P Pearson's correlation; r_S = Spearman rank correlation

CHAPTER IV: DISCUSSION AND RECOMMENDATIONS

4.1 Genetic Implications for Height and Height Growth Curves

4.1.1 Greenhouse and Field Height Growth

During the first growing season, height growth (TH2 to TH18) had consistently high heritability that lacked a specific age trend. As the seedlings entered the second growing season (TH20 to TH36), the pattern of declining heritability with seedling age emerged, though heritability for height remained generally high. In forest trees, it is common for juvenile height to show high heritability (see e.g., Wu et al. 1995), and heritability to change with the age of trees (see e.g., Wu et al. 1995; Xie and Ying 1996; Hodge and White 1992). Sometimes maternal effects may be responsible for high genetic variances and heritability values of growth-related traits such as height of young trees. The most common maternal effect in trees is seed size. Heavy seeds with large embryos, and megagametophytes produce larger seedlings than small seeds. Thus, variation in seed size may cause variation in seedling size, especially during the early stages of the experiment (Evans 1972). Such maternal effects can lead to overestimation of the genetic variance and heritability (Falconer 1981).

Pearson's correlation coefficients between 1000-seed weight and family mean heights were computed to determine the relationship between seed weight and height growth in the greenhouse and in the field. It was revealed that at the end of the first (TH18) and second (TH36) season, correlations between height and 1000-seed weight were 0.421 (*P=0.001*) and 0.433 (*P=0.001*), respectively. The correlations between 1000-seed weight and 11-year height at field site A and B were -0.094 (*P=0.484*) and -0.058 (*P=0.667*), respectively. These correlations indicate a moderate relationship

between seed weight and family means in the greenhouse but not in the field. Thus, variation in seed weight among families might have played a minor role in increasing the genetic variance and heritability for height in the greenhouse but not in the field.

Low genetic variances and heritability values for heights observed in the two field trials were mainly due to excessive site heterogeneity. At site A, the family by block interaction variance for 11-year height was 5.3 times greater than the family variance, whereas at site B, the family by block interaction variance was 17.8 times greater than the family variance. Therefore, nongenetic components of the phenotypic variance masked the genetic variance, leading to low heritability values. Fairly uniform test sites would have yielded greater genetic variances than those observed at the present test sites. Field site B is more favourable for tree growth than site A. The average 11-year height at site B was much larger than that at site A. However, site A had a much larger genetic variance than site B. This suggests that a less favourable site allowed greater expression of genetic differences among families than a favourable site. Although this is not a universal rule, it has been observed in other studies. For example, Li et al. (1991) observed higher heritability values for height, NSU, MSUL and biomass in *Pinus elliottii* at lower than at higher nitrogen treatment. Smith et al. (1993) observed the opposite for the same traits in the same species. Li et al. (1992) observed high heritability for height and summer NSU and MSUL for *Pinus taeda* in the treatment of no watering and no fertilisation as compared to the one with watering and fertilisation. Heritability values for height at the end of the second and third growing seasons were higher in densely than widely spaced experiments of *Pinus sylvestris* (Jonsson et al. 2000).

With low heritability, only moderate to low genetic gain in 11-year height can be expected, unless a very high selection intensity is applied (Zobel and Talbert 1984). This is true for the results of the current study at site A where expected gain for 11-year height was high (15.3%) even though heritability was essentially low (Table 30). On the other hand, a high selection intensity combined with a very low heritability at site B reduced expected gain in 11-year height to only 2.8%. This distinction between selection results at site A and B help to emphasise the fact that response to selection can be expected only when there is an additive genetic variance for the trait under selection (see Griffiths et al. 1993). In addition, expression of different heritability values for the same genetic material at site A and B observed in the current study shows that heritability is a property of the test environment in the same was as it the property of the population and time or age (Falconer 1981).

The age-to-age genetic correlation between the 2-week (TH2) and 36-week (TH36) greenhouse height ($r_A = 0.452 \pm 0.100$) was lower than expected for trees of this age. Even the genetic correlation between 8-week (TH8) and 36-week (TH36) height ($r_A \approx 0.70 \pm 0.06$), which was the highest observed age-to-age correlation, is still low, especially in the relatively uniform greenhouse environment. These low correlations might suggest that a tendency exist for the tested families and families in the Peace River region for which the tested families represent to change ranks in time and space. They might also be indicators of low greenhouse-field genetic correlations, given that the greenhouse and field constitute quite different growth environments.

4.1.2 Growth Curve Parameters

The important parameters of the growth curve for discussion in this study are the absolute rate of growth (r) and age at the point of inflection ($t_{0.5}$). As mentioned in Chapter 1, these parameters provide measures of earliness of growth in height for a given growing season. The upper asymptotic parameter (k) is simply an extrapolated height that the growth curve approaches but never reaches. In organisms with limited life span or animals to be slaughtered only a few weeks or months after birth, k is frequently referred to as mature size or weight. In forest trees, k computed for a given growing season cannot be called mature height of a tree when that tree has a potential to live for more than 100 years. Hence, k is given less consideration for discussion in this thesis. More importantly, values of k for individual seedlings in this study, especially for the first season, were almost the same as the final seasonal height. In this case, it is more meaningful to discuss the correlations of r and $t_{0.5}$ with observed height than with predicted asymptotic height.

Individual-tree heritability values for r and $t_{0.5}$ show that, unlike absolute height, variation in the rate of growth and age at the point of inflection was under low to moderate additive genetic control (Table 6, 7, 8). This supports the finding by Danjon (1994) who observed low heritability for the rate of growth in *Pinus pinaster* Ait. Yeh et al. (unpublished) fitted the logistic function similar to the one fitted in this study, to the first season's data of *Pinus sylvestris* L. from an experiment that was conducted in two growth chambers with different spacing and growth conditions. When data for the two growth chambers were pooled, individual-tree heritability for r was 0.540±0.249 and that of $t_{0.5}$ was 0.699±0.233. In absolute terms, these heritability estimates are larger than those observed in the current study of white spruce. However, in computing heritability,

Yeh et al. (unpublished) multiplied the interclass correlation by 4 rather than the 3 that was used in the current study. When this procedural difference and the size of the standard errors of the estimates are considered, heritabilities for r and $t_{0.5}$ from these two very similar studies are very comparable. Together they shed light on the genetic variability of r and $t_{0.5}$ for seasonal heights of tree seedlings that has rarely been considered in tree breeding.

It should be emphasised here that as far as the growth curve is concerned, absolute height growth is a compound trait that is jointly determined by the rate of growth and time or growth duration. Thus, existence of high heritability for absolute height accompanied by low heritability for individual growth curve parameters is not a contradiction. It simply shows that the genetic variation for absolute height growth cannot be represented by the genetic variation of its component traits taken individually.

Genetic analyses of seasonal growth curves are very rare in forest tree seedlings. Therefore, detailed discussion for the findings of the current study in white spruce necessitates the use of literature from animal genetics, where growth curve analysis has been an almost routine procedure in animal breeding, especially in cattle, chicken and mice. Despite physiological differences that might exist between growth of an animal and that of a tree, the pattern of genetic variation and heritability for parameters of the growth curve observed in white spruce seedlings agree well with those observed in domestic animals and mice. Many of the studies conducted for animal weight show that the rate of growth and age at the point of inflection of the growth curve exhibit low to moderate heritability. A few examples of such studies are cited in Table 37 for comparison with the

corresponding heritability estimates for seedling height observed in the current study of white spruce.

Table 37: Examples of narrow sense heritability for parameters of weight-age growth curves reported in domestic animals

Organism	r	$t_{0.5}$	Author
Mice	0.35	0.41	Kachman et al. (1988)
Sheep	0.21-0.52*		Stobart et al. (1986)
Chicken	0.48	0.18	Barbato (1991)
	0.146-0.671*	0.112-0.880	Grossman and Bohren (1976)
Japanese Quail	0.728, 0.976, 0.480	0.319, 0.412	Akbas and Yaylak (2000)
Cattle	0.19-0.69*		Smith et al. (1976)
	0.21, 0.18	0.24	Telegdi et al. (1980)
	0.20, 0.32		DeNise and Brinks (1985)
	0.27		Jenkins et al. (1991)

* The range of heritability is given where many heritability estimates were reported either at different ages of the organism or heritability varied between male and female groups

It is clear from Table 37 that most heritability values for the rate of growth and age at the point of inflection are low and similar to those observed for white spruce seedlings.

Estimates of heritability for family means in the current white spruce study were high in both growing seasons. The large difference between corresponding heritabilities for the first and second season probably reflects the differences in genetic variability for height growth influenced by differences in modes of growth, i.e., free growth (first season) and predetermined or fixed growth (second season.) Season-to-season results of

growth curve parameters that were observed in this study cannot be used to show age trends in the genetic variance and heritability. This is because growth curves were fitted separately for seasonal height growth increments such that the second-season curves were completely independent of first-season curves. This separate fitting of seasonal curves might also help to explain the differences in the genetic variances and heritability of the growth curve parameters for the two seasons. The first and second season might be considered as being different environments, if there were significant year-to-year differences in growth determining factors such as summer light and temperature that were external to the greenhouse, but nevertheless, influenced conditions in the greenhouse. In this case, seasonal-to-seasonal differences in expression of the genetic variance and heritability for parameters of the growth curve indicate that genetic variance and heritability are properties of the test environment (Falconer 1981).

The genetic correlation for the rate of growth (r) with seasonal asymptotic height (k) and observed first season (FH2-FH18) and second season (SH2-SH18) biweekly cumulative height measurements was between 0.0 and 0.56. This low to moderate genetic correlation contradicts with the very high and near perfect positive correlations observed in mice by Kachman et al. (1988), high correlations observed in *Pinus pinaster* by Danjon (1994), and the negative correlation between r and k ($r_A = -0.225$) observed in *Pinus sylvestris* by Yeh et al. (unpublished). The genetic correlations for r with k and observed height in this study are similar to those reported for body weight in Japanese quail (0.423 and 0.610) (Akbas and Yaylak 2000). In a study involving different breeds of cattle, the genetic correlation between r and body weight at different ages was negative when data for all breeds were pooled (-0.25 to -0.45) and when computed between breeds

(-0.52 to -0.65). However, the correlation was positive (0.22 to 0.36) when computed within breeds (Jenkins et al. 1991). Low negative and positive correlations between *r* and body weight at different ages of ewes were reported by Stobart et al. (1986).

Lack of a strong genetic correlation for *r* with *k* and *r* with final observed seasonal heights (FH18 and SH18) coupled with low individual-tree heritability for *r* suggests that less genetic gain in seasonal height could be achieved by indirect selection for *r* than what could be achieved by direct selection for FH18 or SH18. In addition, the weak genetic correlation between *r* and *k* or *r* with FH18 and SH18 suggests that genotypes with high maximal growth rate did not necessarily achieve greater final height and vice versa. In other words, there exist genotypes in which high rate of growth led to superior final height and those in which high rate of growth did not lead to superior final height. Under this scenario, there are two ways of utilising the relationship between *r* and absolute height:

(a) Selecting for *r* to improve final seasonal height (FH18 and SH18). This could be done by selecting for high values of *r* among families with superior final height. Although the same gain in height might be achieved by selecting for final height alone, selecting for both *r* and final height is important to ensure that selected genotypes are those that achieve height growth at a faster rate (growth/day) as opposed to those that achieve height growth at a long growth duration.

(b) Selecting for *r* to improve early growth without necessarily altering final height (FH18, SH18). This could be done by selecting for high values of *r* with low values of $t_{0.5}$ in a planting stock that is already improved for height growth. This should lead to superior genotypes for height growth with short duration of growth

in which growth is achieved early in the growth season. Developing such genotypes has an advantage of reducing the risk of early fall frost in the planting stock that has already been improved for height growth or volume production. Early growth may also be important in places where competition from weeds is an obstacle to successful seedling establishment. In this case, seedlings from genotypes that are selected for early growth have a better chance of survival than those not selected for early growth.

In this study, the genetic correlation between the age at the point of inflection ($t_{0.5}$) with FH18 and SH18 was 0.262 and 0.428, respectively. The corresponding correlations for $t_{0.5}$ and k for the first and second seasons were 0.289 and 0.554. These low correlations agree with the low correlation (0.378) between $t_{0.5}$ and k in *Pinus sylvestris* observed by Yeh et al. (unpublished). In mice, Kachman et al (1988) observed a lack of genetic correlation for $t_{0.5}$ with k (0.10±0.16) and $t_{0.5}$ with final observed body weight (-0.19±0.14). Akbas and Yaylak (2000) observed a similar lack of genetic correlation between $t_{0.5}$ and k (0.129±0.227 and 0.159±0234) in the Japanese quail. The age at the point of inflection computed in this white spruce study is the age at which the rate of growth is maximum. Thus, lack of strong genetic correlation between $t_{0.5}$ and k or $t_{0.5}$ with FH18 and SH18 is consistent with the fact that r was not strongly correlated with k, FH18 and SH18. In other words, the age at the point of maximum rate of growth did not influence the final seasonal height for most of the genotypes tested.

During the first growing season, the genetic correlation for r with k and FH18 was stronger than that of $t_{0.5}$ with k and FH18. This pattern of correlations was reversed during the second growing season. In this case, the genetic correlation for $t_{0.5}$ with k and

SH18 became stronger than that of r with k and SH18. This might reflect the difference in growth pattern between free growth that occurs after germination to first budset (first season) and fixed or predetermined growth that occurs after free growth in second and subsequent growing seasons. Confirmation of this would require analysis of height growth curves for more than one season of predetermined growth, which could not be done in this study due to serious reductions in the number of seedlings in the third growing season.

In this study, the rate of growth (r) and age at the point of inflection ($t_{0.5}$) were negatively correlated genetically, phenotypically and environmentally. The genetic correlation was lower during the first (-0.192±0.111) than the second (-0.530±0.094) season. Phenotypic and environmental correlations for the two growing seasons were similar. The negative correlation between the rate of growth and age at the point of inflection has been reported in other growth curve studies including those of growth models other than the logistic function, e.g., Kachman et al. (1988), Yeh et al. (unpublished) (r_A = -0.925±0.003), Akbas and Yaylak (2000), Grossman and Bohren (1976), Barbato (1991), Eisen (1976) and Eisen et al. (1969). The negative correlation between the rate of growth and age at the point of inflection implies that genotypes with higher rates of growth reached their point of inflection earlier that those with lower rates of growth. In other words, slow growing genotypes had longer periods of active growth than fast growing ones where the two achieved the same final height or size. If this "antagonistic" relationship between r and $t_{0.5}$ holds true over a number of growing seasons, it would provide a mechanism for genetically improving early growth to escape fall frost damage without necessarily improving seasonal height. This would work by

selecting for high values of r with low values of $t_{0.5}$ in places where the growing season is short and the risk of early fall frost is high.

Although the negative correlation between r and $t_{0.5}$ has widely been observed and is attractive in the tree breeding point of view as indicated in the previous paragraph, it might to a large extent be mathematical rather than biological, i.e., imposed by the way $t_{0.5}$ is computed. For a simple logistic model used in this study, $t_{0.5}$ is the age corresponding to height at *1/2k* and is computed as $t_{0.5} = \frac{1}{r}\log_e b$. In this way, $t_{0.5}$ is inversely proportion to r and the two will change in opposite directions if parameter b is held constant. In other words, the age at the point of inflection will decrease as the rate of growth increases and vice versa. This automatically introduces negative correlation between the two parameters. The strength of the correlation will depend on parameter b. If parameter b is less variable, the negative relationship between r and $t_{0.5}$ will be very strong Note that this is similar to holding b constant thus allowing $t_{0.5}$ to change as r changes. When parameter b is more variable, the negative relationship between r and $t_{0.5}$ will be masked. This dependence of the magnitude of the correlation between r and $t_{0.5}$ on b is exemplified by the very low correlation observed during the first season in which parameter b was very variable genetically, accounting for 17.3% of the total variance (h_i^2=0.557±0.100, h_f^2=0.868±0.181). During the second season, parameter b was less variable genetically, accounting for only 3.2% of the total variance (h_i^2=0.098±0.019, h_f^2=0.356±0.069). This led to a relatively high negative correlation between r and $t_{0.5}$.during the second season compared with the first season. Because of the dependence of the magnitude of the relationship between r and $t_{0.5}$ on the variability in b, the genetic

correlation between r and $t_{0.5}$ might not be of such practical importance as it would otherwise be.

Looking at r and $t_{0.5}$ computed for individual growing seasons in terms of the total height achieved during the entire two-season growth period (TH36), it is clear that r and $t_{0.5}$ influenced TH36 by almost the same magnitude as they influenced total height increment for the season in which they were computed. Other than stem height, growth curve parameters were not correlated, genetically, phenotypically or environmentally with any trait. Unlike height, growth curve parameters were not correlated with seed size (weight).

4.2 Genetic Implications for Other Traits

4.2.1 Root Collar Diameter

Root collar diameter was highly variable genetically as would be expected for young seedlings. Its individual-tree heritability declined gradually with seedling age during the second growing season (D24 to D36) and by the end of the third season it had declined to a low value (Table 16). Much lower heritability values than those observed in this study have been reported for stem diameter in older trees of white spruce (Merrill and Mohn 1985; Yanchuk and Kiss 1993) and also for branch diameter (Merrill and Mohn 1985). The age-to-age genetic correlation between diameter measurements taken at 6-week intervals during the second season remained very high showing that ranking of genotypes for root collar-diameter was stable throughout the second growing season. High genetic correlations between periodic measurements of root collar diameter and stem height show that, to a large extent, genotypes ranked the same for height and diameter during the

entire period of the study. Similar high genetic correlations between height and diameter for older trees of white spruce have been observed in other studies (Tebbetts 1981; Yanchuk and Kiss 1993). Despite the high genetic correlation between height and diameter observed in this study, the rate of growth (*r*) computed from the height growth curve was not correlated in any way with root collar diameter. This suggests that although height and diameter might essentially be the same trait, namely "growth" controlled by the same genes (pleiotropy), their physiological paths of wood formation might be very different.

4.2.2 Biomass Partitioning and Seedling Architecture

Heritability values for fresh and dry weights for different seedling parts (branches, stems, and roots) were generally low (Table 21). Similar low heritability values for fresh and dry weights were also reported in white spruce seedlings by Kharil (1985), *Pinus contorta* seedlings (Wu and Yeh 1997), *Pinus sylvestris* (Velling and Tigerstedt 1984) and *Populus tremuloides* Michx. clones (Lehn and Higginbotham 1982). As stated by Pulkkinene et al. (1989), variation in the process of carbon assimilation with which dry matter accumulates is generally under low genetic control. This is because total dry matter production among families tend to be similar for forest trees, agricultural and forage crops when leaf area and growth conditions are similar. Thus, the low heritability values for fresh and dry matter production observed in this study are consistent with what is expected for many plant species.

In the current study, heritability values for dry weights were slightly higher than the corresponding values for fresh weights. Table 21 shows that the variance component

for the blocking effect was higher for fresh than dry weights. This is probably due to variation in plant tissue moisture among experimental blocks at the time of assessment, since seedling harvesting and weighing was done by experimental blocks. In this case, seedlings in blocks that were harvested one day after watering would have more tissue moisture than those that were harvested two or three days after watering. Thus, studying genetic variation based on plant fresh weight might have a potential for underestimating the genetic variance due to variation in tissue water content, which is a non-genetic component.

The weight for fresh branches, fresh stems, dry branches and dry stems were almost equally correlated genetically, phenotypically, and environmentally with dry weight of roots. In all cases, the genetic correlation was approximately 0.95 or slightly higher (Table 22). This might suggests that either a large root system is needed to supply water and minerals to a large above ground biomass (stem, branches, and needles) or a large above ground biomass generates large photosynthates that in turn promote a large below ground biomass (root system). In a stable environment that favours growth, root and shoot growth tend to be in equilibrium whereby shoot growth triggers a proportional growth in the root system or the other way round (Cannell (1985). Thus, the high genetic correlations for root dry weight with dry weights of branches and main stems that were observed in this study, are indicators of the physiological balance between shoot and root growth in a relatively uniform environment of the greenhouse. In comparison, the genetic correlation between dry weight for branches and roots observed in *Pinus contorta* by Wu and Yeh (1997) was much lower than the corresponding correlation observed in the current white spruce study. However, the correlation between roots and main stem dry

weights in Wu and Yeh (1997) agree well with what was observed in the current white spruce study.

Pearson's correlation coefficients for family means showed that fresh and dry weights for all seedling components were highly correlated with seedling height, diameter, branch length, and to a moderate extent, NSU. The correlations were higher for diameter than height suggesting that both fresh and dry weights were more related to stem and branch diameter than height. Correlations for fresh and dry weights with needle length (NL) and the second season branch length increment (SL) were low but statistically significant. It should be noted that fresh and dry weight especially for the branch component includes a considerable amount of needles. This might be the reason why NL was more correlated with branch fresh and dry weight than the corresponding weights for the stem and roots.

Seedling architecture traits expressed as various ratios of dry weight showed low genetic variability, similar to those expressed by the dry weight components from which they were derived. For example, the harvest index (HI) computed as the proportion of dry weight for the main stem to total above ground dry weight was 0.36 or 36% (family means ranged 0.29 - 0.47). This HI is much greater than that observed in *Pinus sylvestris* by Wu and Yeh (1997), but lower than those reported by Velling and Tigerstedt (1984) also in *Pinus sylvestris*. The heritability of HI reported by Wu and Yeh (1997) is similar to that observed in the current white spruce study, whereas the value reported by Velling and Tigerstedt (1984) is larger than that observed in the current study. It should be understood that the dry weight for branches is the sum of dry weight for needles and branch stems. The contribution of needles to the main stem dry weight can be ignored,

since the amount of needles on the main stem was too small and could probably not be detected on the weighing scale when oven-dried. An attempt to pluck needles from oven-dried branches failed due to breakage of needles and second-order branches. In cases where wood is used for fuel or some form of fibre production that utilises both the main stem and branch stems, the appropriate HI is the proportion of above ground biomass (branches + main stem less needles) to total tree biomass (above + below ground) (Scarascia-Mugnozza et al 1997). This HI could not be computed in this study because needles were not separated from stems, especially on branches. However, it is obvious that such HI would be much larger than the one observed here, though that would not necessarily cause changes in heritability values.

Another ratio of dry weights that is of interest to foresters, especially those dealing with dry land afforestation, is root-shoot ratio, i.e., the ratio of root dry weight to above ground dry weight. In this study, the root-shoot ratio averaged 0.39 (range of family means 0.29 - 0.50). This ratio is considered by foresters to be an indicator of the ability of the root system of the tree to extract enough water from the soil to sustain transpiring vegetative parts. At the time of establishment of seedlings in the field, a large value of root-shoot ratio is preferred as it indicates the presence of a large root system relative to the vegetative part for which it supplies water and minerals from the soil. Nevertheless, root-shoot ratios computed without separation of the lateral roots from the taproot may not be good indicators of the plant water and nutrient extraction capacity as the taproot mainly plays a supportive role rather than water or nutrient absorption. This drawback may be serious in species with well developed taproots and less of a problem in species with less developed taproots such as white spruce (Den Ouden and Boom 1965;

Hosie 1969). In the constant environment where growth conditions are favourable, the root and shoot systems are in equilibrium such that the root and shoot relative growth rates tend to be constant. Under this equilibrium, assimilates are preferentially used by shoots if growth conditions limit photosynthesis or by roots if conditions limit nutrient or water uptake (Cannell 1985). It appears then that this natural mechanism to maintain a balance between water uptake and transpiration makes root-shoot ratio a trait directly linked to fitness as it influences reproduction and survival of the species in dry habitats. It is known that traits directly involved in reproductive fitness exhibit low additive genetic variance, and thus low narrow sense heritability (Falconer 1981). This might explain the cause of low heritability for the root-shoot ratio observed in the current white spruce study and other similar studies (see eg. Wu and Yeh 1997).

The ratio of dry weight for the main stem to dry weight for branches (BI) showed that on average, biomass production of branches was 40% greater than biomass production of the main stem. Individual-tree heritability for BI was low (0.201) suggesting that selection for BI would result to only a small response. The average ratio of branch length to total seedling height (CS) was 0.51 indicating that the average seedling height after two seasons of growth was approximately twice the average branch length. The individual tree heritability was generally low (0.286) whereas heritability for family means was high (0.655). In this study and other similar studies (see e.g., Rweyongeza 1997), branch length was found to be highly positively genetically correlated with tree height. This means it would be difficult to reduce branch size to improve wood quality or to increase wood yield on the main stem relative to the branches (sny HI) without suppressing height growth. Thus, selecting for lower values of CS in

genotypes of above average stem height may be the only feasible way of eliminating undesirably thick and long branches. Otherwise, silvicultural measures such as spacing control and pruning may be more effective.

In this study, the stem slender quotient (ST) also called sturdiness (see Wu and Yeh 1997) was computed both as the ratio of height (TH36) to diameter (D36) and denoted ST* and as the ratio of D36 to TH36 and denoted ST. Analysis of variance showed that ST* had no statistically significant genetic variance and all variation was entirely environmental. Contrary, ST was genetically variable with the family variance accounting for 12.7% of the total variance and the narrow sense heritability of 0.393. This was true for both data in original and standard units. Thus, the stem slender quotient presented in this thesis is $ST = D36/TH36$. In addition to being statistically significant, this formulation of stem slender quotient renders itself to a better interpretation than the one expressed as $ST^* = TH36/D36$. This is because ST ranges from 0 to 1 whereas ST* has no definite range. In *Pinus sylvestris* Velling and Tigerstedt (1984) and Wu and Yeh (1997) expressed stem slender quotient using ST* formulation and obtained narrow sense heritability of 0.26 and 0.315, respectively. Both heritabilities are lower than the one observed in the current study of white spruce. According to Wu and Yeh (1997), the slender quotient expressed as ST* is an indicator of tree-taper in mature trees. In a different formulation, Wu (1994) computed stem taper in *Populus* hybrids as *1-(stem diameter at 6m/DBH)*, where DBH stands for diameter at breast height (1.3m). Thus there may be different formulations of stem taper other than those cited here.

This study showed that Pearson's correlation coefficients for family means for the ratios of dry weights, CS, and ST with TH36, D36, D54, BL, NL, NSU SL were

generally low or medium. Some of these correlations were negative (Table 29). It is important to remember that these correlations exist simply because BD, DS, TDS, DR from which the dry weight ratios were derived, were highly correlated with TH36, D36, D54, BL, NL, NSU and SL. Taking partial correlations between dry weight ratios and TH36, D36, D54, BL, NL, NSU and SL while controlling for the influence of BD, DS, TDS, DR reduces the correlations between dry weight ratios and TH36, D36, D54, BL, NL, NSU and SL to almost zero.

4.2.3 Dates for Budburst

This study showed that the date for budburst had medium individual-tree heritability and high heritability for family means (Table 19). To the contrary, Wilkinson (1977) found low heritability values for budburst in white spruce. Nienstaedt (1985) reported a much higher heritability in white spruce than the ones observed in the current study. The date for budburst was not correlated in any way with stem height. It was slightly correlated genetically with root collar diameter, but when the standard errors of the correlation coefficients are considered, these correlations are not far from zero. Li et al. (1977) reported a genetic correlation of -0.65 between height and the date for budburst and 0.77 between height and the date for budset. Chapter 1 provided a detailed review of the relationship between height and phenological traits (dates for budburst and budset) and the duration of the growing season, especially at the population level. In this study, the dates for budset were not recorded. As a result, the growth duration for the families tested is not known. Therefore, results of this study cannot rule out the possibility that the height reached by families might be related to their growth duration.

4.2.4 Branch and Needle Lengths

The average needle length was correlated genetically and phenotypically with the first season's total height (FH18) (r_A = 0.292±0.092, r_P = 0.264), second season's total height increment (SH18) (r_A = 0.729±0.050, r_P = 0.461), 36-week total height (TH36) (r_A = 0.642±0.061, r_P = 0.480), 36-week root collar diameter (D36) (r_A = 0.542±0.074, r_P = 0.470), and average branch length (BL) (r_A = 0.409±0.086, r_P = 0.412). These predominantly medium positive genetic correlations between needle length and growth-related traits, i.e., height, diameter and branch length suggest that growth potential could be moderately improved by indirect selection for longer needles. In *Pinus sylvestris*, Rweyongeza (1997) found negative genetic correlations between growth-related traits and needle length, suggesting that growth potential could be reduced by selecting for longer needles or improved by selecting for shorter needles. In a *Pinus sylvestris* provenance study, Ruby and Wright (1976) found no correlation between growth traits and needle length. Since needles mature much earlier than height and diameter, the existence of a strong and stable genetic association between growth potential and length of needles would be very useful in identification of potentially superior genotypes at young stages.

Branch length was correlated genetically with height (TH36) (r_A = 0.871±0.026) and root collar diameter (r_A = 0.720±0.051), suggesting that selection to increase both height and diameter growth would lead to long, and possibly thick, branches. Like stem height, branch length was not correlated genetically with the date for budburst on primary branches (r_A = -0.116±0.099). Thus, selection for the date of budburst would not affect branch length.

4.2.5 Tissue Components

In this study, the number of stem units (NSU) and mean stem unit length (MSUL) had low individual-tree heritability. Numerous studies of variation in stem tissue components have been conducted in *Pinus* species and can help to explain the findings of the current white spruce study. For example, Kremer and Larson (1983) studied tissue components in *Pinus banksiana* Lamb. under two temperature regimes. Heritability values for NSU and MSUL were higher at lower, than at higher temperature. Also heritability values were higher during the first season (free growth) at both temperature regimes than during the second season (fixed growth). At both temperature regimes, the heritability values expressed during the second season were low and similar to those observed in the current study of white spruce. Li et al. (1991) studied tissue components in *Pinus taeda* L. under high and low nitrogen levels. Heritability for NSU was much higher at low than at high nitrogen level. There was no statistically significant genetic variability for MSUL. Li et al. (1992) studied tissue components in *Pinus taeda* L under two combinations of fertilisation and watering regimes. Both NSU and MSUL had low heritability values similar to those observed in the current white spruce study. In the study of *Picea pungens* Engelm. Bongarten (1986) observed low heritability for NSU and heritability of 1.01 for MSUL. Jonsson et al. (2000) studied tissue components in *Pinus sylvestris* under wide and narrow spacing. Heritability values were high for NSU and low for MSUL at both spacing levels. Smith et al. (1993) studied variation in tissue components in *Pinus elliottii* Engelm. under high and low nitrogen during free and cyclic growths (sny. fixed growth). Heritability values for NSU and MSUL were higher at high than at low nitrogen level. Also, estimates of heritability were higher during free than cyclic growth period. The

heritability values observed by Smith et al. (1993) during the cyclic period support the low heritability for NSU and MSUL observed for white spruce in the current study.

The estimates of heritability cited above generally show that both NSU and MSUL tended to have low heritability, which is consistent with the low heritability values observed in the current study of white spruce. However, it appears that the amount of genetic variability, and consequently heritability, can vary greatly under different test conditions, i.e., temperature, moisture regime and probably any other environmental factor. Estimates of heritability for tissue components in the present study were made only for one growth condition and one growing season. Thus, whether these heritability values would change from season to season or with varying environmental conditions or not is the question that the present study cannot answer.

Genetic correlations and genetic degrees of determination show that MSUL, rather than NSU, was the greater determinant of the annual branch increment (SL) in white spruce families tested in this study. However, the importance of MSUL over NSU is not overwhelming and it is, therefore, reasonable to conclude that both MSUL and NSU were important in determining the size of the branch increment attained during the second season. The importance of both NSU and MSUL in determining SL makes sense since longer stem units alone could not lead to longer SL if there were only very few stem units to elongate. In *Picea pungens*, Bongarten (1986) found that MSUL was a much greater determinant of SL than NSU at a family level. At the provenance level, NSU was more important than MSUL. In *Pseudotsuga menziesii* var *glauca* (Beissn) Franco. provenances, Bongarten (1986) found that MSUL was more important than NSU in some groups of provenances, whereas in other groups of provenances NSU was more

important than MSUL. However, in both cases the correlation between NSU and SL was not overwhelming over that of MSUL and SL or vice versa. This suggests that both NSU and MSUL were important in determining SL in the primary branches of *Pseudotsuga menziesii*. While studying *Pinus banksiana*, Kremer and Larson (1983) found that NSU and MSUL were equally important at high temperature during the second season. At low temperature, NSU was overwhelmingly more important than MSUL. In the first season shoot, NSU and MSUL were equally important at lower temperature, whereas at higher temperature MSUL was more important than NSU. Note that, despite some inconsistencies for results at different temperatures and growing seasons, the findings by Kremer and Larson (1983) largely support the idea that both NSU and MSUL are important in determining SL. In *Pinus elliottii*, Smith et al. (1993) found that at a high nitrogen level, cyclic SL was more correlated genetically with MSUL (0.80±0.49) than NSU (0.50±0.19). However, looking at the two correlations in terms of standard errors, we can conclude that both NSU and MSUL were important in determining cyclic SL.

In the present white spruce study, NSU and MSUL were generally not correlated genetically when the standard error of the correlation coefficient is considered. Phenotypic and environmental correlations between the two were also very low suggesting that the two tissue components might be genetically, phenotypically and environmentally independent. This contradicts with the results by Smith et al. (1993) who reported strong positive genetic correlations between NSU and MSUL in *Pinus elliottii*, Kremer and Larson (1983) who observed strong negative correlations in *Pinus banksiana* and Bongarten (1986) who found negative correlations in *Picea pungens* and *Pseudotsuga menziesii*.

Analysis of tissue components in the present study also shows that the second season branch increment (SL) from which NSU and MSUL were assessed was highly correlated genetically with the total first season's main stem height (FH18), second season's total main stem height increment (SH18) and 36-week main stem height (TH36). This was clearly expected since total branch length (BL) was correlated genetically with FH18, SH18 and TH36. An interesting observation is that NSU was correlated genetically with only SH18 and TH36, whereas MSUL was correlated genetically with FH18, SH18 and TH36 with almost similar magnitude. The existence of a strong genetic correlation between MSUL and FH18 and lack of a reasonable genetic correlation between NSU and FH18 suggest that MSUL rather than NSU is a better trait in characterising genotypic growth. Note that SL and SH18 were largely predetermined growth laid down in terms of stem units during the previous season. Thus, correlation of NSU and MSUL (assessed from SL) with SH18 and TH36 can be expected. To the contrary, FH18 was formed during the first season as the result of free growth and was not correlated in any way with SH18. Yet MSUL was correlated genetically with FH18 with similar magnitude as the correlation between MSUL and SH18 or MSUL and TH36. NSU lacked a genetic correlation with FH18 but was correlated with it phenotypically and environmentally. This suggests that variation in NSU is more environmental than genetic, whereas variation in MSUL is more genetic than environmental. This argument is supported by the fact that in this study the heritability for MSUL was almost twice that of NSU.

4.3 Feasibility of Early Selection

Previous sections have dealt with variation, heritability, genetic correlations and their implications to selection and breeding to improve juvenile growth as was studied in the greenhouse. However, a very important component of tree breeding is to link ranking of potentially desirable genotypes in the greenhouse and their long term ranking in the field. It is this link that is at the core of a search for juvenile traits that are indicators of better field performance.

In this study, much higher genetic gains from direct selection for 10- and 11-year heights could be expected at site A than at site B (Table 30). The additive genetic variance and heritability values at site B were too low to produce meaningful expected genetic gains from direct selection for height at age 10 and 11 years when compared to site A. The feasibility of early selection in this study is measured by the selection efficiency, i.e., the ratio of correlated gain (gain expected from indirect selection for juvenile greenhouse traits) to gain from direct selection (gain from direct selection for 10- or 11-year heights). Since gains from direct selection (denominator) at site B were very low, selection efficiencies for site B appears to be much higher than the corresponding values for site A, even though correlated gains (numerator) were much higher at site A than at site B.

It should clearly be understood that selection efficiency is a relative measure. Thus, a high selection efficiency value can have meaningful interpretation, only when correlated gain is compared with a meaningful gain from direct selection. If efficiency of selection is high, largely due to very low gain from direct selection caused by lack of genetic variation in the trait targeted for improvement as it was the case for site B, a high

selection efficiency value will be misleading. In this case, the correlated gain, which is an absolute measure of the gain expected for 10- and 11-year height as a result of indirect selection on juvenile greenhouse trait (Table 33) provided a better measure of the feasibility of early selection than the selection efficiency. Therefore, when discussing the feasibility of early selection in this thesis using efficiencies of selection, reference will be made to the results at site A and not site B. This is meant to avoid exaggerating the prospects of early selection even in cases where it is almost nil. Since all the results involving site B are included in the thesis, readers and potential users of the information contained in this thesis may wish to make their own interpretation of the selection efficiencies involving site B.

When field site A and all 58 families were considered, it was apparent that selecting families for improving 10- and 11-year heights based on juvenile greenhouse traits would have very low to moderate efficiency. This was true for almost all juvenile traits assessed in this study. The highest predicted efficiency of early selection for the 10- and 11-year height was 56.5% and 55.5%, respectively, expected from selection for 14-week (FH14) greenhouse height. When early selection is considered on gain per generation as opposed to gain per year, these efficiencies of early selection are low, considering the fact that juvenile greenhouse height had very high heritability values at all ages. The second highest efficiency of early selection for 10- and 11-year height was 34.7% and 33.6%, respectively, expected from selection for mean stem unit length (MSUL). Note that the genetic correlation between MSUL and field height was higher than that of greenhouse height and field height. However, the heritability for MSUL was

much lower than that of greenhouse height. This made MSUL a much less efficient predictor of field height than greenhouse height.

To better predict field height, the juvenile trait needs to have both high heritability and a reasonably high genetic correlation with field height (Falconer 1981). It is obvious that lack of predictability of field height by juvenile traits in this study when all 58 families were involved was due to serious rank changes for height in the greenhouse and the field. This caused low greenhouse-field genetic correlations for all traits. This was confirmed by the fact that exclusion of 15 families, whose rank changes for the greenhouse TH36 and field height at age 11 years were considered too extreme, improved greenhouse-field genetic correlations for almost all traits. Exclusion of these families also revealed an orderly trend in age-to-age genetic correlations between greenhouse and field height that was obscured when all 58 families were involved.

If selection were to be done within 43 families that are subset of the original 58 families, early selection for cumulative juvenile greenhouse height would be very efficient in improving field height at age 10 and 11 years. In this case, efficiency of early selection for first season cumulative biweekly height would range from 45.3% (FH2) to 114.3% (FH18) for 10-year height, and 47.4% (FH2) to 108.4% (FH18) for 11-year height. Unlike selection efficiencies computed from 58 families where efficiency of selection for cumulative biweekly height declined sharply after the first season, selection efficiencies involving 43 families were high even after the first growth season (TH20 to TH36) Here selection efficiency for biweekly cumulative height ranged 114.2% to 96.9% for 10-year height, and 110.4% to 87.9% for 11-year height.

Table 34 shows that selection efficiency for greenhouse height increased with seedling age from age 2 to 18 weeks after germination (first season or FH2 to FH18). When seedlings entered the second season (TH20 to TH36), selection efficiency initially increased with seedling age between age 20 (TH20) and 24 (TH24) weeks after germination, and thereafter declined with seedling age to the end of the second season, i.e., around age 34 (TH34) and 36 (TH36) weeks after germination. The age trend of the selection efficiency for the first 18 weeks of the study (first season) is consistent with what is expected, since the genetic correlation between early and late traits should increase as the age gap between the two measurements narrows. Despite unexpected decrease in selection efficiency for cumulative biweekly height after the first season, it can be concluded that within a subset of 43 families, selection for cumulative biweekly height would be very efficient in improving 10- and 11-year height at site A, if selection was conducted with seedlings of any age between 6 and 36 weeks after seed germination (Table 34).

Selection for second season height increment alone (SH2 to SH18) would capture 54.9% to 74.5% of the genetic gain expected from direct selection for field height at age 10 years and 48.8% to 63.3% for field height 11 years. Selection for MSUL and branch length (BL) would yield 87.6% and 62.6%, respectively, of the gain expected from direct selection for height at age 11 years. Indirect early selection for root collar diameter and needle length (NL) would be moderately efficient in predicting field height. For root collar diameter, selection efficiency of 34% to 58.5% is a great improvement, since with 58 families, it was predicted that selection for second season diameter would depress 11-year height by 2.4-11.5%. With 45.2% and 39% efficiency, the number of stem units

(NSU) had a drastic improvement in the prediction of AH10 and HA11, respectively, compared with the selection efficiencies of 5.6% and 3.2% when all 58 families were involved.

Unlike absolute height, the growth curve parameters r and $t_{0.5}$ were not good predictors for field height. The first season $t_{0.5}$ and second season r would capture only 39% of gain expected from direct selection for height at age 11 years, when families with extreme rank changes are excluded. In this case, first season $t_{0.5}$ achieved this efficiency because of its high heritability, whereas second season r achieved this efficiency because of its moderate genetic correlation with field height. Low efficiency of early selection for r and $t_{0.5}$ is consistent with the fact that these two parameters had low or moderate genetic correlation with greenhouse juvenile height. Their heritability values were also low leading to low correlated gains. Another explanation for this might be that the r and $t_{0.5}$ predicted for one season of free growth and one season of fixed growth cannot adequately represent height growth accrued over the period of 10 and 11 years (growing seasons) during which growth was predominantly fixed or predetermined. Therefore, studies of growth curves for many seasons of fixed growth might be necessary to establish a meaningful relationship between seasonal r and $t_{0.5}$ with total height accrued over many growing seasons, and the worthiness of r and $t_{0.5}$ as early selection indicators.

Selection indices combining three greenhouse traits to predict expected gain in 11-year height, when all 58 families were included in the analysis using site A as an example, were less efficient than one would expect. Table 35 shows that the selection indices combining total height at the end of the first season (FH18), maximum rate of growth for the first growing season (r or R_1), age at the point of inflection during the first

season ($t_{0.5}$ or $T0_1$) and the date for terminal bud burst (TB2) were less efficient than selection based on FH18 alone (Table 34). This discrepancy is explained as follows: In computing correlated genetic gains from single trait selection, genetic correlations between greenhouse traits and field height were calculated on an individual trait basis. This allowed traits such as first season heights to use all of their data points (≈1670). In this large dataset the correlation between FH18 and AH11 was approximately 0.3 and heritability for AH11 was 0.231. For selection indices, different traits were combined for computing variances and covariances. As a result the dataset was reduced to 1300. In this reduced dataset the correlation between FH18 and AH11 declined to about 0.2, whereas the heritability for AH11 increased to about 0.28. This means correlated gain declined while gain from direct selection on AH11 increased causing reduction in efficiency of selection. Correlations between *r* and AH11 or TB2 and AH11 were not strong enough to compensate for the loss of correlation between AH11 and FH18. Selection indices that included MSUL had better results partly because of high heritability since variation among branches within family was not considered, as was the case before.

Selection indices involving the trait targeted for improvement are meant to use information from relatives (siblings) or other traits to supplement the information on the trait to be improved (Becker 1975; Falconer 1981). Thus, such selection indices yield additional gain on top of the gain expected from direct selection on the target trait alone. This can be visualised from the following hypothetical selection index:

$$I = b_1Y + b_2X,$$

Where, Y is the trait to be improved, X is the trait that is correlated with Y, b_1 and b_2 are coefficients (weights) computed for trait Y and X, respectively. If we rescale (see Becker

1975; Falconer 1981) this selection index by dividing the right side of the equation by b_1 and letting $b_2/b_1 = b_3$, the index reduces to:

$$I = Y + b_3X$$

This shows that even with marginal genetic correlation, additional information from even one trait will produce additional gain above the gain expected from selection on the target trait alone. Wu et al. (2000) presented the following expression for combining field trait with one juvenile trait from a retrospective study:

$$R_{I,y} = \sqrt{1 + \frac{(r_p - r_g \frac{h_x}{h_y})^2}{1 - r_p^2}}$$

Where, $R_{I,y}$ is the selection efficiency for a selection index that combine trait Y as a target trait and trait X as juvenile trait from a retrospective study, r_g and r_p are genetic and phenotypic correlations between Y and X, h_x and h_y are square roots of the heritabilities for trait X and Y, respectively. Provided the phenotypic correlation (r_p) between traits Y and X is within the permissible range (-1 to 1), the part of the expression on the right side of the plus sign will be positive suggesting that $R_{I,A}$ will always be equal or greater than 1.0. In other words, combining information on early and late traits will always produce more genetic gain for the late trait than selection based on the late trait alone. This highlights an important point that even in cases where retrospective studies are unable to identify juvenile traits that are by themselves satisfactory selection criteria for mature field traits, they still can furnish very useful information that, in combination with the mature traits, will yield greater gain than selection based on the mature trait alone.

In this study, gain efficiencies from index selection that combined information on AH11 and two greenhouse traits were modest (1-8%) when compared with similar

indices reported for *Pinus contorta* in Alberta by Wu et al. (2000). However, if these selection indices were to be constructed for the 43 families as previously indicated, gain efficiencies would be much higher than those observed when all 58 families were involved.

There are reports in the literature of forest genetics that either support or refute the prospects of early selection. In *Pinus radiata* D. Don, King and Burdon (1991) predicted that selection for breast height diameter (DBH) at 5 years would produce 75% of the gain expected from direct selection for DBH at 17 years. Index selection based on DBH at age 5 and 10 years would capture 100% of the gain expected from direct selection at age 17 years. Foster (1986) found that selection based on height and survival at age 3 years would produce 81% of the gain expected from direct selection for volume at age 15 years in *Pinus elliottii*. In *Pseudotsuga menziesii*, Bastien and Roman-Amat (1990) showed that selection for 2-year height and 8-year basal area were, respectively, 69% and 87% efficient in improving volume production at age 15 years. Index selection combining 8-year height and basal area would produce 89% of gain from direct selection for volume at age 15 years. Gill (1987) studied early selection in *Picea sitchensis* (Bong.) Carr. and found that selection for 1-year height would produce only 37.2% of the gain expected from direct selection for 10-year height. However, selection for 3-year height would capture 91.5% of gain from direct selection for 10-year height. Selection done at age 6-years would increase this efficiency to 96.7%.

Jonsson et al. (2000) reported on early selection in *Pinus sylvestris* from a study carried out in the phytotron under wide and dense spacing. Results generally showed that juvenile traits would better predict the 28-year height and volume when assessed under

wide than dense spacing. Under wide spacing, the 3-year height was the best predictor of 28-year height (96.3%) and volume (93.1%). Height at age 1 and 2-years, and 3-year traits such as 3-year height increment, MSUL, basal diameter, above ground fresh weight, shoot and needle dry weight, and stem dry weight would produce between 64% and 80% of the gain expected from direct selection for 28-year height, and 56%-84% for 28-year volume production. The coefficient of genetic prediction for 15-year volume by 3-year height in *Platanus occidentalis* L. was estimated at 0.58 (Green and Lowe 1992). In the same species, Nebgen and Lowe (1985) reported that family selection for 1-year height predicted 61% and 87% of the gain expected from direct selection for 7-year height and volume, respectively. Lambeth et al. (1983) found that in *Pinus taeda* early family selection for 20-year volume was efficient as early as age 5-years, whereas selection for 20-year volume based on individual trees was efficient at 10 years. Note that this study also showed that genetic correlations between 5 and 20-year heights were very high, except in a few cases where the correlation was greater than 1.0 making it less meaningful.

In *Pinus taeda*, Li et al. (1992) found that in a watered and fertilised treatment 2 and 3-year heights would produce 81% and 82%, respectively, of the gain expected from direct selection for 8-year height. In this case, 1-year height would not efficiently predict 8-year height (26%). Li et al. (1992) also showed that while summer NSU would produce 87% of the gain from direct selection for 8-year height, summer MSUL would depress the same height by 55%. They also showed that both fixed NSU and MSUL would depress 8-year height. By studying *Pinus eliottii* under low and high nitrogen treatments, Smith et al. (1993) found that first-year height, NSU and MSUL were not individually

good predictors of 15-year volume. Combining these juvenile traits in multitrait indices would efficiently predict the 15-year volume. In *Pinus contorta* Doug., Xie and Ying (1996) reported that efficiencies of early selection per year of tree improvement for 24-year stem volume were highest when selection was done for 7-year height, 14-year DBH, and 14-years stem volume. However, this is expected, since selection efficiency per year will tend to increase with the increase in the ratio between later (advanced) and early (young) ages. This increase in the gap between the selection year for a juvenile trait and the targeted year for selection of a "mature" or advanced age trait makes early selection more efficient than mature selection in terms of gain per year (Lambeth 1980).

McKeand (1988) showed that in *Pinus taeda* gain per year for a 25-year rotation was maximised by early selection between 3 and 10 years, and that with fair assumptions on the change of heritability and age-to-age genetic correlations with time, selection age would be optimised between 6 and 8 years. This was supported by Balocchi et al. (1994), who used the present value under the 8% discount rate and 26-year rotation age criteria to predict the optimum selection age for the same species. In a different study of *Pinus taeda*, Balocchi et al. (1993) observed low coefficients of genetic prediction for the 26-year height by height measurements at young ages. Even at 16 years, the additive coefficient of genetic prediction for half-sib and full-sib families was approximately 0.6. This suggests that selection for 26-year height would not be efficiently done at young ages.

In *Pinus radiata*, Cotterill and Dean (1988) estimated a genetic correlation of 0.24 between 2.5-year and 10.5year height, whereas the correlation between 2.5-year and 16.5-year heights was -0.12 in the unthinned stand. In the thinned stand, the genetic

correlation between 2.5-year and 10.5-year height was 0.31. The correlation between 6.5-year and 10.6-year in the thinned stand was almost perfect (r_A = 0.99). These correlations suggest that selection for height at a much younger age would not be effective in improving advanced age height. In *Pinus elliottii*, Squillace and Gansel (1974) found that height at age 3 was poorly correlated genetically with height at age 25 years. However, the genetic correlations improved greatly after age 8, and it was predicted that the greatest gain from early selection to improve the 25-year height would be realised at age 10 years of field growth or age 14 years from seed. In *Pinus taeda*, Williams (1987) found that height before the first budset (free growth) was negatively correlated with 8-year height. To the contrary, height after the first budset (cyclic growth) was positively correlated with 8-year height (r_A = 0.59). The genetic correlations between dry weight and 8-year height ranged from negative to zero.

More studies can be cited here to corroborate the findings of the current study of early selection in white spruce. However, those reports cited here are enough to make general conclusions about early selection results of the current study of white spruce. It is obvious that the efficiency of early selection observed for the first season greenhouse height and height at field site A (AH10 and AH11) when all 58 families were involved in the analysis are in good agreement with those observed in other forest tree species.

The selection efficiencies of 53.5% and 52.2% expected from selection for height at the end of the first season (FH18) for improving 10- and 11-year height, respectively, at site A when all 58 family were involved, are moderate when genetic gain is considered on a generation basis. These selection efficiencies show that approximately 50% of gain expected from selection at the ages of 10 and 11 years would be forfeited in the process

of shortening the breeding cycle. However, when gain is considered on per year basis, these selection efficiencies are very high, since they represent gains or returns from one year of breeding efforts.

It is understood that correlated gain per generation from early selection as in other cases of indirect selection cannot be higher than gain from direct selection unless the genetic correlation between the two traits is high and the young trait has higher heritability than the older trait (Falconer 1981). If selection for a young trait has to cause response in a mature trait, a high genetic correlation (preferably from pleiotropic gene action) between young and mature trait is necessary. Since selection is applied on the phenotype rather than genotype, a high heritability is necessary; otherwise phenotypic selection will be ineffective. It is obvious that in many studies where early selection appeared promising, the higher correlated gains have been due to high heritability values for the juvenile traits. This is particularly true for the results of the current study in white spruce. It should be remembered that even after excluding families with extreme rank changes from the analyses, the greenhouse-field genetic correlation for height at site A did not exceed 0.6. Despite these reasonably low age-to-age genetic correlations, correlated gains in field height expected from mass selection on juvenile heights were very high and in other cases higher than gains expected from direct selection on field height. This was possibly largely due to high heritability values for greenhouse height especially during the first growing season. It follows from this fact that since heritability is expected to decline with age of trees, efficiencies of early selection observed in this study would have declined in response to changing heritability of juvenile height had the

experiment been extended to four or more years. Thus, one should exercise caution in interpreting and using early selection findings from this study.

Many of the cited studies show that early selection is possible as early as five years depending on the anticipated plantation rotation age. However, most of these studies were conducted in *Pinus* species, which have shorter rotations than white spruce. In addition, many of these studies have been conducted in warmer areas of southern and southeastern USA where growth periods are longer than that in northern Alberta. Thus, one should exercise caution in comparing the findings of the current study in white spruce with those in published reports, since at 5 years in a warm climate a pine tree may be several times larger than a white spruce sapling in northern Alberta such that the biology of the two cannot be fairly compared.

For the purpose of improving experimental techniques in the future, it is always good to try to speculate on the factors that might have produced the current results. The model formulated by Lambeth (1980) to predict age-to-age genetic correlations showed that for different conifers, age-to-age correlations involving very young ages were not predictable. Lambeth (1980) considered this to be due to the time taken for families to adjust themselves to the new growing conditions in the field that are different from the growing conditions in the nursery or greenhouse where the families were raised prior to field planting. This would apply to correlations involving ages 1 and 2 with advanced ages similar to those involved in the current study of white spruce. However, the time to adjust to field conditions may not be applicable here, since the current white spruce study is a retrospective one in which greenhouse and field plants are different, but came from the same families and seed collections.

Variation in seed size among the families tested could also cause lack of good correlation between greenhouse and field height by altering family ranks. It was mentioned earlier that height growth in the greenhouse had a statistically significant positive correlation with 1000-seed weight, and that 1000-seed weight was not correlated with field height. This influence of seed weight on juvenile traits but not on field height would be expected to affect the correspondence in ranking of families between the greenhouse and the field experiments. However, a close examination of the data suggests that this might not clearly be the case. After excluding the 15 families with serious rank changes between the greenhouse and the field, the correlation between TH36 and 1000-seed weight remained almost the same as that in 58 families. In addition, the correlation between TH36 and 1000-seed weight in the 15 excluded families was 0.414 which is approximately the same as that in the original population of 58 families ($r = 0.433$). Thus, although variation in seed weight has been suspected elsewhere in altering juvenile-mature correlations (see, e.g., Riitters and Perry 1987) it might not be the reason for rank changes observed in the current study.

The current study in white spruce was conducted in the greenhouse with fairly controlled day length, night temperature, nutrition, and moisture. The day length was longer in the greenhouse than in the field. Nutrients provided in the greenhouse were designed to maximise vegetative growth during the growth period and root growth during the hardening period. Greenhouse seedlings are shielded from large-scale day-to-day weather fluctuations and undesirable levels of essential and nonessential minerals. These are ideal growing conditions rarely encountered in the field. Thus, growth and survival in these two contrasting environments might involve the action of quite different genes or

gene-environment interaction (Falconer 1981). This study also showed that there was a strong genotype by environment (GE) interaction between the two field test sites.

The realisation of the importance of the similarities between the testing environments in enhancing juvenile-mature correlations in the retrospective studies has led to attempts by researchers to try to replicate field conditions in the greenhouses and growth chambers (see e.g., Cannell et al. 1978; Eriksson et al. 1993; Jonsson et al. 2000). The idea is to identify one or two most growth-limiting factors in the field experiment that can be adequately reproduced in indoor experiments. No restrictions were imposed on any of the growth conditions in the greenhouse for the current study. Thus, lack of relationship between the field and greenhouse growth conditions might be one of the reasons for poor greenhouse-field correlations.

The use of extended photoperiod as opposed to normal day length and natural light has been suspected to alter ranking of families between greenhouse/growth chambers and field experiments (see, e.g., Bongarten and Hanover 1985; Pharis et al. 1991, Pharis pers. comm.). Extended photoperiod was used in this study, and therefore remains one of the possible causes of poor greenhouse-field correlations. Pharis et al. (1991) also provides some insight on the possible hormone actions that might explain the presence or absence of correlations between young indoor and old field experiments.

The data for both field experiments (A and B) and the greenhouse do not provide clues on the possible cause of poor correlation between greenhouse and field performance. Appendix 7 presents multiple comparisons for TH36, AH11 and BH11 using Duncan's New Multiple Range Test at 95% level of probability. The 15 families with serious rank changes that were excluded in the second phase of analysis do not form

a group that would differentiate them from other families. There was such a large overlap in the family means that it was difficult to notice the differences among families. A close examination of the growth curve parameters for these families, especially that of the first season one (Appendix 3), shows that 14 of the 15 families were characterised by below average maximum rate of growth (r), and their age at the point of inflection ($t_{0.5}$) was around the population mean. Although these 15 families appear to have the same type of growth curves in the greenhouse, it would be difficult to link it with poor greenhouse-field ranking, since no such information exists for the material that was tested in the field. However, if growth patterns of these families in the field were different from those observed for their siblings in the greenhouse, this too could be the cause of poor greenhouse-field correlations.

Other possible factors that would affect the correspondence in ranking of families between the greenhouse and field experiments include ontogeny (see e.g., Falconer, 1981; Cheverud et al. 1983; Williams 1987; Namkoong et al. 1988), in which expression of height growth between 11-year old field growing trees and 1 or 2-year old seedlings in the greenhouse might not be controlled by the same set of genes because of age and size differences; post-planting shock (Lambeth 1980); and biotic or abiotic factors for the field experiments.

Abiotic factors are such things as microsite differences. It was indicated earlier that the block by family interaction variance was 5.6 and 17.8 times greater than the family variance component at site A and B, respectively. This suggests that the test sites were heterogeneous in many ways. If in this case a family plot is located on a better or poorer plot, it may affect the overall mean of the family and, thus, affect its ranking in the

field compared to the greenhouse where growth conditions are fairy uniform. Biotic factors are such things as damage by pine weevils. The damage by pine weevils is common in Alberta Forest Service white spruce experiments. My experience with data from these trials show that the average height in a population of trees that have had damage by pine weevils is significantly lower that that of the general population. Thus, in analysing the data for field trials and for greenhouse-field correlations trees that had positive score for pine weevils (approximately 5% of the data) were excluded. This improved the correlations between greenhouse and field performance. However, if there were incidences of weevil damage in early years and trees recovered from this damage, it might take years for trees to compensate for the lost growth potential. This may still affect the current greenhouse-field correlations even if the trees look normal.

The range of environments to which the results of early selection from this study can be applied depends on the magnitude of the genotype by environment (GE) interaction (Falconer 1981). Analysis of data from the two field trials showed that high GE interaction existed between site A and B, though type B genetic correlations (see Burdon 1977) computed for 10- and 11-year height between site A and B might suggest otherwise. It is important to note that these correlations are in large errors by the mere fact that they are well out of the permissible range for the correlation coefficient (-1 to +1) (Table 36). The most likely cause of such out of range genetic correlations is lack of sufficient genetic variances at both site A and B. Thus, the true picture of the correspondence of family ranks between the two sites is given by Pearson's correlations and Spearman's rank correlations of family means (Table 36). Both types of correlations were between 0.36 and 0.40 showing that the strong family by site interaction revealed by

the analysis of variance during the joint analysis of site A and B was due to rank changes. There was also evidence of GE interaction in the greenhouse results, which shows that the first and second season height increments were not correlated. This is a form of GE interaction in the form of family by year interaction. Although genotype by year interaction is not relevant in forestry, since annual variations in family ranks are averaged over many decades of tree growth (Burdon 1977), it might signal the possible existence of the family by site interaction that is relevant in tree breeding.

Wu et al. (1997) reported a strong GE interaction for the four test sites of *Pinus contorta* in Alberta. A GE interaction was also evident in *Pinus sylvestris* progeny trials at three test sites in Alberta (Rweyongeza 1997). Thus, there is clear evidence to suggest that the strong GE interaction observed for white spruce progeny test is the norm rather than exception. Practically, it shows that genotype selections on one site may not be automatically used on other test sites that are evidently ecologically different from the site where selection took place (Falconer 1981; Wu et al. 1997). In addition, it highlights the need for controlling some of the growth-limiting variables to enhance greenhouse-field correlations in the retrospective greenhouse and growth chamber studies.

The existence of a strong GE interaction between the two field trials points to another important factor in early selection involving retrospective studies. The genetic correlation between field and greenhouse traits computed in retrospective studies is of type B (correlation between traits measured on different individuals of the same family) rather than type A (correlation between traits measured on the same individual). As indicated in Chapter 2, the type B genetic correlation between greenhouse traits and field height that was used in this study was computed from the mean squares according to

Robertson (1959). This correlation can also be computed from the variance components as expressed by Yamada (1962), (also see Burdon 1977) in the following formula:

$$r_g = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{sf}^2}$$

where r_g = genetic correlation between two traits measured on different individuals of the same family raised in different environments, σ_f^2 = among -family variance component, and σ_{sf}^2 = site by family interaction variance component or GE interaction variance component. This expression clearly shows that the genetic correlation depends on the magnitude of the GE interaction. Therefore, it can be concluded that for early selection based on type B genetic correlation to be efficient, the GE interaction between field- and indoor-assessed traits has to be kept to a minimum or tolerable level. This highlights the need for controlling some of the growth-limiting variables to enhancing greenhouse-field correlation by reducing the family by site interaction component.

4.4 General Conclusions

In view of the foregoing results and discussions, the following general conclusions can be made from the current white spruce study:

1. By this study, it was possible to establish the mechanisms by which individual seedlings and families attained their seasonal height. The study showed that seasonal growth of white spruce seedlings in partially controlled growth environments could be accurately described by many of the familiar growth functions that follows a sigmoid pattern of growth. The maximum absolute rate of growth (r) and age at the point of inflection ($t_{0.5}$), which is the age at which r is

maximum were less genetically variable than height and poorly or moderately correlated genetically with the final seasonal height.

2. Although the mean stem unit length (MSUL) was more correlated genetically with height growth than the number of stem units (NSU) was, both NSU and MSUL were important joint determinants of height growth in white spruce. The argument is that enough stem units should be deposited and that these stem units should have long intervals between them (MSUL) if the genotype has to achieve superior seasonal height growth.

3. The only juvenile greenhouse trait that had good prediction of gain in field height when all 58 families were involved was height growth during the first growing season (FH2 to FH18). Considering the time factor, first growing season height, MSUL and to some extent needle length (NL), might yield even better results when field conditions are mimicked in the greenhouse.

4. Lack of correlation between almost all greenhouse traits and field height was due to large-scale rank changes between greenhouse height and field heights. If correlations were improved by identifying critical growth limiting factors and replicating them in the greenhouse, many of the assessed greenhouse traits would serve as good selection criteria for field height. This was evidenced by the great improvement in magnitude and direction of the correlations when families with serious rank changes were excluded from the analyses.

5. It was clearly observed that high heritability values of greenhouse traits played a great role in boosting efficiencies of early selection in the current study. Thus, caution should be taken not to overemphasise the prospects of early selection

from this study, since heritabilities do change with age and test environments. Emphasis should be directed toward improving juvenile-mature genetic correlations.

4.5 Recommendations

1. The results from the current study should be used for making family selections to improve height at site A, and probably other sites that are ecologically very similar to site A. However, stringent conditions should be placed on rank stability for the families. This will counteract the influence of high heritability values of juvenile traits on correlated genetic gains. If results from all 58 families are to be used, only the first season height (FH18) should be used as a selection criterion.
2. Early selection results from 43 families that are a subset of the original 58 families can also be used for selection to improve height at site A and other very similar sites, though these results were obtained by deliberately excluding some families from the analysis. My interpretation is that there is a pattern in the data that support the existence of good greenhouse-field correlations for most of the traits. This pattern is simply obscured by the presence in the data of some families whose ranks for height across sites were extremely unstable.
3. Follow-up reassessment of field tests is needed to see if meaningful genetic variances have emerged that would cast a good picture on the prospects of early selection. This is particularly important for field site B where plant survival and growth were good but genetic variability was almost non-existent. In addition, the field data used in this study were taken almost five years ago and need to be

updated. Because of this time lag, the results in this thesis might not represent the current situation on the ground.

4. Analyses of seasonal height growth curves occupied a greater portion of this study and the results suggest that for growth curve parameters k, r and $t_{0.5}$, family ranks might not be stable from one season to another (greater genotype by season interaction). Therefore, similar studies in the future should consider extending the experiments beyond two growing seasons so that growth curves of at least two seasons of fixed growth and one season of free growth could be fitted. In the current study, data for the first season (free growth) fitted all growth functions much easier than data for the second season (fixed growth). If data were available for the third or even fourth season (fixed growth), we could be able to answer the following questions:

   (a) Is the observed family rank instability for seasonal height growth curve parameters caused by the differences in growth patterns between free growth and fixed growth or just a general tendency for these parameters to exhibit great genotype by environment interaction?

   (b) Is seasonal height growth during fixed growth periods consistently harder to predict than height growth during the free growth period?

   Note that keeping vigorous seedlings for three or four seasons would require larger containers than those used in the current study. This is necessary to avoid having the plants become root bound that would arrest height growth in an experiment that relies on uninterrupted height growth. It would also require a safer way of preserving seedlings during winter to avoid large losses of seedlings

through terminal dieback that severely reduce the sample size. Also, the study could be replicated in more than one growth condition so that genotype by environment interaction other than genotype by growing season (year) interaction for the growth curve parameters could be studied.

5. To enhance greenhouse-field genetic correlations, future retrospective tests should avoid use of extended photoperiods, since there are indications that traits such as root collar diameter are well correlated genetically with field height when seedlings are raised under natural day length (Dr. R. P. Pharis personal comm.). There must also be attempts to identify and mimic critical field growth conditions in the greenhouse as a way of reducing environmental differences between greenhouse retrospective studies and field studies. Factors such as moisture, nutrients, temperature, photoperiod, and spacing can be manipulated in the greenhouse or growth chamber to mimic the corresponding factors at the field test sites.

LITERATURE CITED

Akbas, Y., and Yaylak, E. 2000. Heritability estimates of growth curve parameters and genetic correlations between the growth curve parameters and weight at different ages of Japanese quail. Arch. Geflugelk. **64**: 141-146.

Anonymous 1948. Wood-plant seed manual. USDA For. Serv. Miscellaneous publication No. 654.

Balocchi, C. E., Bridgewater, F. E., Zobel, B. J., and Jahromi, S. 1993. Age trends in genetic parameters for tree height in a nonselected population of loblolly pine. Forest Sci. **39**: 231-251.

Balocchi, C. E., Bridgewater, F. E., and Bryant, R. 1994. Selection efficiency in a nonselected population of loblolly pine. Forest Sci. **40**: 452-473.

Barbato, G. F. 1991. Genetic architecture of growth curve parameters in chickens. Theor. Appl. Genet. **83**: 24-32.

Bastien, J. C. H., and Roman-Amat, B. 1990. Predicting Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) volume at age 15 with early traits. Silvae Genetica **39**: 29-35.

Becker, W. A. 1975. Manual of quantitative genetics. Washington State University Press. Pullman. Washington.

Blum, B. M. 1988. Variation in the phenology of bud flushing in white and red spruce. Can. J. For. Res. **18**: 315-319.

Bongarten, B. 1986. Relationship between shoot length and shoot length components in Douglas-fir and blue spruce. Can. J. For. Res. **16**: 373-380.

Bongarten, B. C., and Hanover, J. W. 1985. Accelerating seedling growth through photoperiod extension for genetic testing. A case study with blue spruce (*Picea pungens*). Forest Sci. **31**: 631-643.

Borralho, N. M. G., Kanowski, P. J., and Cotterill, P. P. 1992. Genetic control of growth of Eucalyptus globulus in Portugal: I. Genetic and phenotypic parameters. Silvae Genetica 41:39-45.

Brown, J. E., Fitzhugh, H. A., and Cartwright, T. C. 1976. A comparison of nonlinear models for describing weight-age relationship in cattle. J. Animal Sci. **42**:810-818.

Burdon, R. D., and Sweet, G. B. 1976. The problem of interpreting inherent differences in tree growth shortly after planting. *In* Tree Physiology and Yield Improvement. *Edited by* M. G. R. Cannell and F. T. Last. Academic Press. London. pp 483-502.

Burdon, R. D. 1977. Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genetica **26**: 168-175.

Cannell, M. G. R. 1985. Dry matter partitioning in tree crops. *In* Attributes of trees as crop plants. *Edited by* M. G. R. Cannell and J. E. Jackson. Institute of Terrestrial Ecology. Penicuik, Scotland. pp 160-193.

Cannell, M. G. R., Bridgewater, F. E., and Greenwood, M. S. 1978. Seedling growth rates, water stress response and root-shoot relationship related to eight-year volume among families of *Pinus taeda* L. Silvae Genetica **27**: 237-247.

Cheliak, W. M., Pitel, J. A., and Murray, G. 1985. Population structure and the mating system of white spruce. Can. J. For. Res. **15**:301-308.

Cheverud, J. M., Rutledge, J. J., and Atchley, W. R. 1983. Quantitative genetics of development: Genetic correlations among age-specific trait values and the evolution of ontogeny. Evolution **37**:895-905.

Coles, J. F., and Fowler, D. P. 1976. Inbreeding in neighbouring trees of two white spruce populations. Silvae Genetica 25: 29-34.

Corriveau, A., Beaulieu, J., and Mothe, F. 1987. Wood density of natural white spruce populations in Quebec. Can. J. For. Res. **17**: 675-682.

Cotterill, P. P., and Dean, C. A. 1988. Changes in the genetic control of Radiata pine to 16 years and efficiencies of early selection. Silvae Genetica **37**: 138-147.

Danjon, F. 1994. Heritabilities and genetic correlations for estimated growth curve parameters in maritime pine. Theor. Appl. Genet. **89**: 911-921.

Daubenmire, R. 1974. Taxonomic and ecological relationship between *Picea glauca* and *Picea engelmannii*. Can. J. Bot. **52**:1545-1560.

Den Ouden, P., and Boom, B. K. 1965. Manual of cultivated conifers. Martinus Nijhoff, The Hague.

DeNise, R. S. K., and Brinks, J. S. 1985. Genetic and environmental aspects of growth curve parameters in beef cows. J. Animal Sci. **61**: 1461-1440.

Doak, C. C. 1935. Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. Illinois Biological Monographs 13. Urbana. Illinois.

Eisen, E. J., Lang, B. J., and Legates, J. E. 1969. Comparison of growth functions within and between lines of mice selected for large and small body weight. Theor. Appl. Genet. **39**: 251-260.

Eisen, E. J. 1976. Results of growth curve analysis in mice and rats. J. Anim. Sci. **42**: 1008-1023.

Eriksson, G., Jonsson, A., Domling, I., Norell, L., and Stener, L –G. 1993. Retrospective early tests of *pinus sylvestris* L. seedlings grown under five nutrient regimes. Forest Sci. **39**: 95-117.

Evans, G. C. 1972. The quantitative analysis of plant growth. Blackwell Scientific Publications. Oxford.

Falconer, D. S. 1981. Introduction to quantitative genetics. 2st Edition. Longman Inc. New York.

Fowler, D. P., and Park, Y. S. 1983. Population studies of white spruce. I. Effects of self-pollination. Can. J. For. Res. **13**:1133-1138.

Franklin, E. C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genetica **28**:207-212.

Furnier, G. R., Stine, M., Mohn, C. A., and Clyde, M. A. 1991. Geographic patterns of variation in allozymes and height growth in white spruce. Can. J. For. Res. **21**: 707-712.

Furnier, G. R., and Stine, M. 1995. Interpopulation differentiation in nuclear and chloroplast loci in white spruce. Can. J. For. Res. **25**: 736-742.

Gill, J. G. S. 1987. Juvenile-mature correlations and trends in genetic variances in sitka spruce in Britain. Silvae Genetica **36**: 189-194.

Green, T. A., and Lowe, W. J. 1992. Changes in the pattern of genetic variability over time in American sycamore and the implication for early selection. Can. J. For. Res. **22**: 713-717.

Griffiths, A. J. F., Miller, J. H., Suzuki, D. T., Lowontin, R. C., and Gelbart, W. M. 1993. An introduction to genetic analysis. 5th Ed. W. H. Freeman and Company. New York.

Grossman, M., and Bohren, B. B. 1976. Logistic growth curve of chickens: Heritability of parameters. J. Heredity **76**: 459-462.

Hall, J. P. 1986. Provenance trial of white spruce in Newfoundland: Twenty five years from seed. Can. For. Serv. Newfoundland Res. Cent. Inf. Rep. N-X-247.

Hodge, G. R., and White, T. L. 1992. Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. Silvae Genetica **41**: 252-262.

Hosie R. C. 1969. Native trees of Canada. 7th Ed. Can. For. Serv. Ottawa.

Jenkins, T. G., Kaps, M., Cundiff, L. V., and Ferrell, C. L. 1991. Evaluation of between- and within-breed variation in measures of weight-age relationship. J. Anim. Sci. **69**: 3118-3128.

Jonsson, A., Eriksson, G., Ye, Z., and Yeh, F. C. 2000. A retrospective early test of *Pinus sylvestris* seedlings grown at a wide and dense spacing. Can. J. For. Res. **30**:1443-1452.

Kachman, S. D., Baker, R. L., and Gianola, D. 1988. Phenotypic and genetic variability of estimated growth curve parameters in mice. Theor. Appl. Genet. **76**: 148-156.

Khalil, M. A. K. 1985. Heritability of juvenile characters of white spruce (Picea glauca (Moench.) Voss.) in central Newfoundland, Canada. Theor. Appl. Genet. **69**: 247-251.

Khalil, M. A. K. 1986. Variation in seed quality and juvenile characters of white spruce (*Picea glauca* (Moench) Voss). Sivae Genetica **35**: 78-85.

King, J. N., Dancik, B. P., and Dhir, N. K. 1984. Genetic structure and mating system of white spruce (*Picea glauca*) in a seed production area. Can. J. For. Res. **14**:639-643.

King, J. N., and Burdon, R. D. 1991. Time trends in inheritance and projected efficiencies of early selection in a large-17-year old progeny test of *Pinus radiata*. Can. J. For. Res. **21**: 1200-1207.

Kotov M. M. 1989. Winter hardiness, drought resistance and growth rate of Scotch pine grafts in geographic plantations of the Mari ASSR. Soviet For. Sci. **6**:20-24.

Kremer, A., and Larson, P. R. 1983. Genetic control of height growth components in jack pine seedlings. Forest Sci. **29**: 451-464.

Kremer, A. 1992. Prediction of age-age correlation of total height based on serial correlations between height increments in maritime pine (*Pinus pinaster* Ait.). Theor. Appl. Genet. **85**: 152-158.

Lambeth C. C. 1980. Juvenile-mature correlations in *Pinaceae* and implications for early selection. Forest Sci. **26**: 571-580.

Lambeth, C. C., Van Buijtenen, J. P., Duke, S. D., and McCullough, R. B. 1983. Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genetica **32**: 210-215.

Lehn, G. A., and Higginbotham, K. O. 1982. Natural variation in merchantable stem biomass and volume among clones of *Populus tremuloides* Michx. Can. J. For. Res. **12**: 83-89.

Li, P., Beaurieu, J., and Bousquet, J. 1977. Genetic structure and patterns of genetic variation among populations in eastern white spruce (*Picea glauca*). Can. J. For. Res. **27**: 189-198.

Li, B., McKeand, S. E., and Allen, H. L. 1991. Seedling shoot growth of loblolly pine families under two nitrogen levels as related to 12-year height. Can. J. For. Res. **21**: 842-847.

Li, B., Williams, C. G., Carlson, W. C., Harrington, C. A., and Lambeth, C. C. 1992. Gain efficiency in short-term testing: experimental results. Can. J. For. Res. **22**: 290-297.

Li, P., Beaulieu, J., Corriveau, A., and Bousquet, J. 1993. Genetic variation in juvenile growth and phenology in a white spruce provenance-progeny test. Silvae Genetica **42**: 52-60.

Lopez de Torre, G., and Rankin, B. J. 1978. Factors affecting growth curve parameters of Horeford and Brangus cows. J. Animal Sci. **46**: 604-613.

Magnussen, S. 1988. Minimum age-to-age correlations in early selection. Forest Sci. **34**: 928-938.

Magnussen, S., and Kremer. A. 1993. Selection for an optimum tree growth curve. Silvae Genetica **42**: 322-334.

Magnussen, S., and Yanchuk A. D. 1993. Selection age and risk: Finding the compromise. Silvae Genetica **42**: 25-40.

McKeand, S. E. 1988. Optimum age for family selection for growth in genetic tests of loblolly pine. Forest Sci. **34**: 400-411.

Mergen, F., Burley, J., and Furnival, G. 1965. Embryo and seedling development in *Picea glauca* (Moench) Voss. after self-, cross-, and wind-pollination. Silvae Genetica. **14**:188-194.

Merrill, R. E., and Mohn, C. A. 1985. Heritability and genetic correlations for stem diameter and branch characteristics in white spruce. Can. J. For. Res. **15**: 494-497.

Mikola, J. 1982. Bud-set phenology as an indicator of climatic adaptation of Scots pine Finland. Silva Fennica **16**: 178-182.

Mosseler, A., Egger, K. N., and Hughes, G. A. 1992. Low levels of genetic diversity in red pine confirmed by random amplified polymorphic DNA markers. Can. J. For. Res. **22**: 1332-1337.

Nair, K. R. 1954. The fitting of growth curves. *In* Statistics and Mathematics in Biology. *Edited by* O. Kempthorne. Iowa State University. Ames. pp 119-133.

Nalder, J. A. 1961. The fitting of a generalization of the logistic curve. Biometrics **17**: 89-110.

Namkoong. G., Kang, H. C and Brouard, J. S. 1988. Tree breeding: Principles and strategies. Monographs on Theoretical and Applied Genetics. Springer-Verlag. New York.

Nebgen, R. J., and Lowe, W. J. 1985. The efficiency of early and indirect selection in three sycamore genetic tests Silvae Genetica **34**: 72-75.

Nienstaedt, H. 1985. Inheritance and correlations of frost injury, growth, flowering and cone characteristics in white spruce (*Picea glauca* (Moench) Voss. Can. J. For. Res. **15**: 498-504.

Nienstaedt, H., and Riemenschneider, D. E. 1985. Changes in heritability estimates with age and site in white spruce, *Picea glauca* (Moench) Voss. Silvae Genetica **34**: 34-41.

O'Reilly, C., and Parker, W. H. 1982. Vegetative phenology in a clonal seed orchard of *Picea glauca* and *Picea mariana* in northwestern Ontario. Can. J. For. Res. **12**: 408-413.

Park, Y. S., Fowler, D. P., and Coles, J. F. 1984. Population studies of white spruce. II. Natural inbreeding and relatedness among neighbouring trees. Can. J. For. Res. **14**:909-913.

Pharis, R. P., Yeh, F. C., and Dancik, B. P. 1991. Superior growth potential in trees: What is its basis, and can it be tested for at an early stage? Can. J. For. Res. **21**: 368-374.

Pollard, D. F. W., and Ying, C. C. 1979a. Variation in response to declining photoperiod among families and stands of white spruce in southeastern Ontario. Can. J. For. Res. **9**: 443-448.

Pollard, D. F. W., and Ying, C. C. 1979b. Variance in flushing among and within stands of seedling white spruce. Can. J. For. Res. **9**: 517-521.

Pulkkinen, P., Poykko, T., Tigerstedt, P. M. A., and Velling, P. 1989. Harvest index in northern temperate cultivated conifers. Tree Physiology **5**: 83-98.

Rajora, O. P., and Dancik, B. P. 2000. Population genetic variation, structure, and evolution in Engelmann spruce, white spruce, and their natural hybrid complex in Alberta. Can. J. Bot. **78**: 768-780.

Rehfeldt, G. E. 1983a. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. III. Central Idaho. Can. J. For. Res. 13: 626-632.

Rehfeldt, G. E. 1983b. Adaptation of *Pinus contorta* populations to heterogeneous environments in northern Idaho. Can. J. For. Res. 13: 405-411.

Rehfeldt, G. E. 1988. Ecological genetics of *Pinus contorta* from the Rocky mountains (USA): a synthesis. Silvae Genetica, **37**: 131-135.

Richards, F. J. 1959. A flexible growth function for empirical use. J. Exper. Bot. **10**: 290-300.

Ritters, K. H., and Perry, D. A. 1987. Early genetic evaluation of open-pollinated Douglas-fir families. Forest Sci. **33**: 577-582.

Robertson, A. 1959: The sampling variance of the genetic correlation coefficient. Biometrics **15**: 469-485.

Roche, L. 1969. A genecological study of the genus *Picea* in British Columbia. New Phytology **68**:505-554.

Rowe, J. S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Department of Northern Affairs and Natural Resources. Forest Research Division Technical Note No. 3.

Ruby, J. L., and Wright, J. W. 1976. A revised classification of geographic varieties in Scotch pine. Silvae Genetica **25**: 169-175.

Rweyongeza, D. M. 1997. A study of geographic and genetic variation of Scots pine (*Pinus sylvestris L.*). M.Sc. Thesis. University of Alberta. Edmonton.

Sargent, C. P. 1926. Manual of the trees of North America. Houghton Mifflin Company. Boston and New York.

SAS Institute Inc. 1994. SAS system for windows. Cary. North Carolina.

Scarascia-Mugnozza, G. E., Ceulemans, R., Heilman, P. E., Isebrands, J. G., Stettler, R. F., and Hinckley, T. M. Production physiology and morphology of *Populus* species and their hybrids grown under short rotation. II. Biomass components and harvest index of hybrid and parental species clones. Can. J. For. Res. **27**: 285-294.

Scoggan, H. J. 1978. The flora of Canada. Part II. National Museum of Natural Science. Ottawa.

Smith, G. M., Fitzhugh, H. A., Cundiff, L. V., Cartwright, T. C., and Gregory, K. E. 1976. A genetic analysis of maturing patterns in straightbred and crossbred Hereford, Angus and Shorthorn cattle. J. Anim. Sci. **43**: 389-395.

Smith, C. K., White, T. L., Hodge, G. R., Duryea, M. L., and Long, A. J. 1993. Genetic variation in first-year slash pine shoot components and their relationship to mature field performance. Can. J. For. Res. **23**: 1557-1565.

Squillace, A. E., and Gansel, C. R. 1974. Juvenile:mature correlations in slash pine. Forest Sci. **20**: 225-229.

Sterllrecht, J. W., Mohn, C. A and Cromell, W. M. 1974. Productivity of white spruce seed sources in Minnesota test planting. Minnesota Forestry Research Notes No. 251.

Stiell, W. M. 1976. White spruce: Artificial regeneration in Canada. Can. For. Serv. Inf. Rep. FMR-X-85.

Stobart, R. H., Bassett, J. W., Cartwright, T. C., and Blackwell, R. L. 1986. An analysis of body weight and maturing patterns in western range ewes. J. Anim. Sci. **63**: 729-740.

Taylor, F. W., Wang, E. I. C., Yanchuk, A., and Micko, M. M. 1982. Specific gravity and tracheid length variation of white spruce in Alberta. Can. J. For. Res. **12**: 561-566.

Tebbetts, R. P. 1981. Early results of Ottawa valley white spruce progeny test planted in Maine. *In* Proceedings of the 2nd North Central Tree Improvement Conference, 5-7 August 1992, Lincoln, Nebraska. pp 140-146.

Teich, A. H., Skeates, D. A., Morgenstern, E. K. 1975. Performance of white spruce provenances in Ontario. Special Joint Report No. 1. Petawawa National Forest Institute, Environment Canada and Ontario Ministry of Natural Resources.

Telegdi, L., Andersen, B. B., and Thysen, I. 1980. Fitting and genetic analysis of growth curves for young bulls. Acta Agronomica Academiae Scientiarum Hungaricae **29**: 13-23.

Tremblay, M., and Simon, J –P. 1989. Genetic structure of marginal populations of white spruce (*Picea glauca*) at its northern limit of distribution in Nouveau-Quebec. Can. J. For. Res. **19**: 1371-1379.

Velling, P., and Tigerstedt, M. A. Harvest index in a progeny test of Scots pine with preference to the model of selection. Silva Fennica **18**: 21-32.

Wilkinson, R. C. 1977. Inheritance of budbreak and correlation with early height growth in white spruce (*Picea glauca*) from New England. USDA For. Serv. Res. Pap. NE-391.

Williams, C. G. 1987. The influence of shoot ontogeny on juvenile-mature correlations in loblolly pine. Forest Sci. **33**: 411-422.

Wright, J. W. 1955. Species crossability in spruce in relation to distribution and taxonomy. Forest Sci. **1**:319-345.

Wright, J. W. 1964. Flowering age of clonal and seedling trees as a factor in choice of breeding system. Silvae Genetica **13**: 21-27.

Wright, J. W. 1976. Introduction to forest genetics. Academic Press. New York.

Wright, J. W., and Bull, W. I. 1963. Geographic variation in Scotch pine: Results of the 3-year Michigan study. Silvae Genetica **12**: 1-25.

Wright, J. W., Kung, F. H., Read, R. A., Lemmien, W. A., and Bright, J. N. 1971. Geographic variation in Rocky mountain Douglas-fir. Silvae Genetica, **20**: 54-60.

Wu, R. –L. 1994. Quantitative genetics of yield breeding for *Populus* short rotation culture. III. Efficiency of indirect selection on tree geometry. Ther. Appl. Genet. **88**: 803-811.

Wu, H. X., and Yeh, F. C. 1997. Genetic effect on biomass partition and tree architecture in seedlings of *Pinus contorta* spp. *latifolia*, in Alberta, Canada. Forest Genetics **4**: 123-130.

Wu, H. X., Yeh, F. C., Pharis, R. P., Dancik, B. P. Jiang, I. B., Dymock, I., and Dhir, N. K. 1995. Genetic parameters of greenhouse growth and performance of 2-year *Pinus contorta* subsp. *Latifolia*. Scand. J. For. Res. **10**: 12-21.

Wu, H. X., Yeh, F. C., Dhir, N. K., Pharis, R. P., and Dancik, B. P. 1997. Genotype by environment interaction and genetic correlation of greenhouse and field performance in *Pinus contorta* ssp. *latifolia*. Silvae Genetica **46**: 170-175.

Wu, H. X., Yeh, F. C., Dancik, B. P., Pharis, R. P., and Dhir, N. K. 2000. Study of early selection in tree breeding: 3. A case study using early information to enhance selection efficiency in later trait in lodgepole pine. Silvae Genetica **49**: 152-158.

Xie, C. –Y., and Ying, C. C. 1996. Heritabilities, age-age correlations, and early selection in lodgepole pine (*Pinus contorta* ssp. *latifolia*). Silvae Genetica **45**: 101-107.

Yamada, Y. 1962. Genotype by environment interaction and genetic correlation of the same trait under different environments. Japan. J. Genet. **37**: 498-509.

Yanchuk, A. D., and Kiss, G. K. 1993. Genetic variation in growth and wood specific gravity and its utility in the improvement of interior spruce in British Columbia. Silvae Genetica **42**: 141-148.

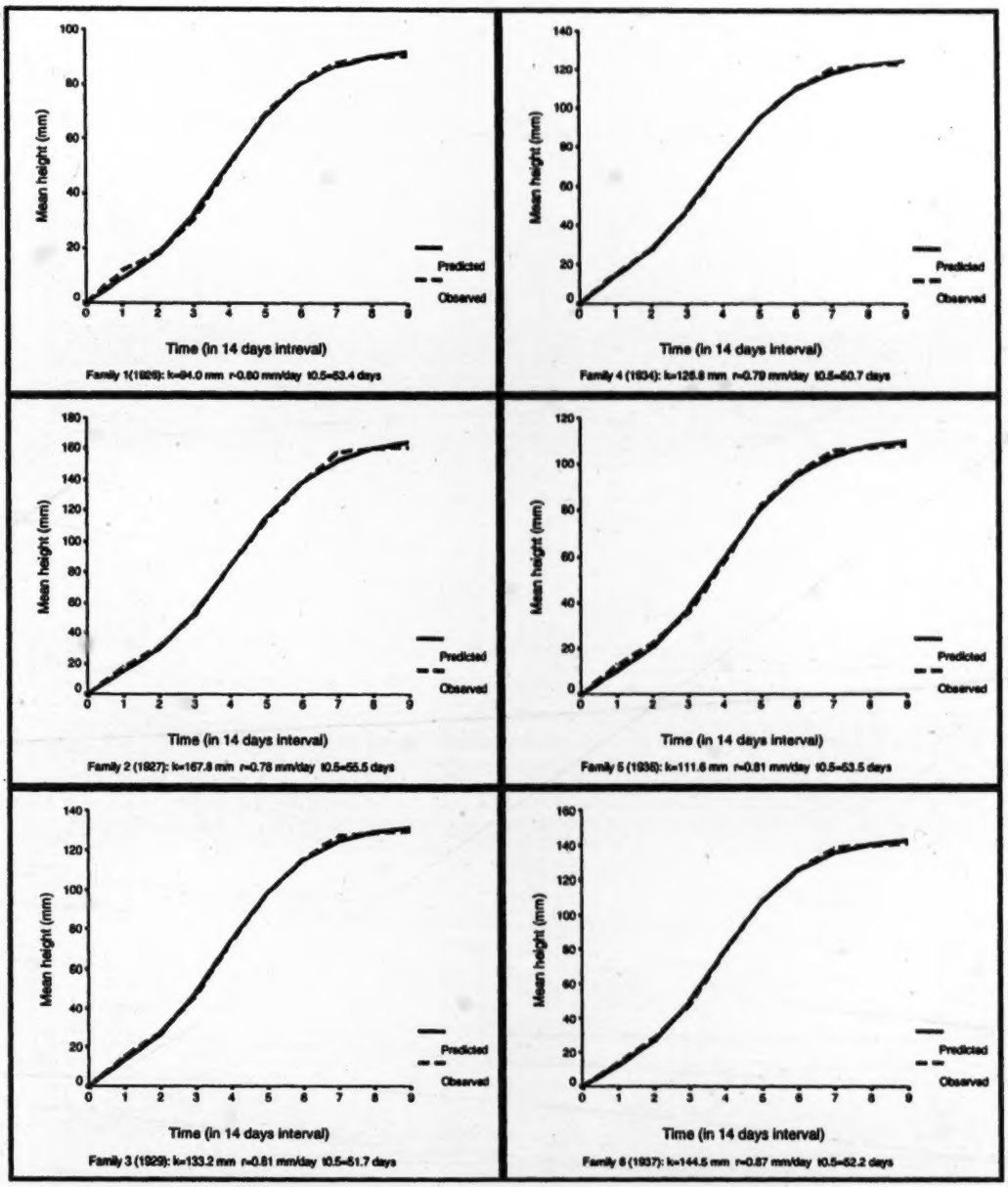
Zobel, B. J., and Talbert, J. T. 1984. Applied forest tree improvement. John Wiley and sons. New York.

Appendix 1: Seedlot accession numbers and geographic locations for the families tested in this study.

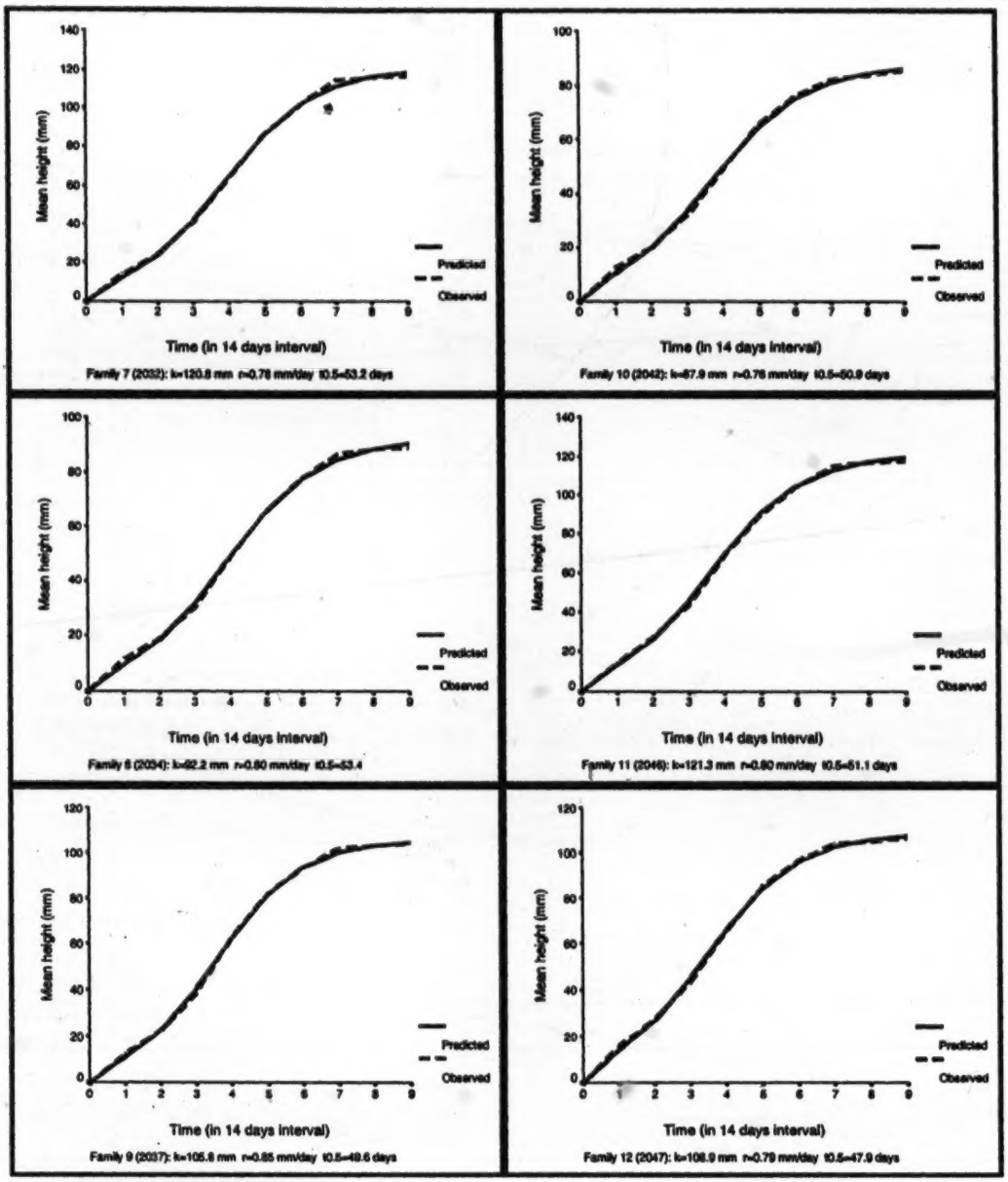
Family	Alberta FS Accession No.	Latitude (N)	Longitude (W)	Elevation (m)
1	1926	50° 24'	119° 29'	520
2	1927	50° 24'	119° 29'	520
3	1929	56° 17'	119° 11'	400
4	1934	56° 16'	119° 16'	425
5	1936	56° 15'	119° 02'	400
6	1937	56° 17'	119° 12'	400
7	2032	55° 29'	118° 46'	945
8	2034	55° 29'	118° 46'	945
9	2037	55° 29'	118° 39'	815
10	2042	55° 32'	119° 25'	855
11	2046	55° 29'	119° 34'	845
12	2047	55° 29'	119° 35'	870
13	2048	55° 38'	119° 44'	855
14	2050	55° 38'	119° 44'	825
15	2051	55° 39'	119° 46'	780
16	2053	55° 35'	119° 31'	885
17	2054	55° 35'	119° 32'	885
18	2342	54° 31'	118° 42'	885
19	2343	54° 38'	118° 37'	75
20	2344	54° 37'	118° 37'	805
21	2347	55° 39'	119° 37'	775
22	2349	55° 38'	119° 41'	850
23	2351	55° 34'	119° 21'	915
24	2352	55° 41'	119° 22'	850
25	2355	55° 33'	119° 52'	832
26	2357	55° 35'	119° 55'	854
27	2358	55° 35'	119° 47'	869
28	2359	55° 29'	118° 50'	945
31	2452	55° 34'	119° 22'	880
32	2454	55° 38'	119° 41'	850
33	2455	55° 38'	119° 41'	850
34	2457	55° 45'	119° 54'	822
35	2458	55° 41'	119° 29'	810
36	2461	55° 41'	119° 22'	884
37	2462	55° 48'	119° 45'	730
38	2463	55° 48'	119° 45'	730
39	2464	55° 48'	119° 44'	745
40	2465	55° 34'	119° 26'	840
41	2466	55° 34'	119° 26'	840

Appendix 1: Continues

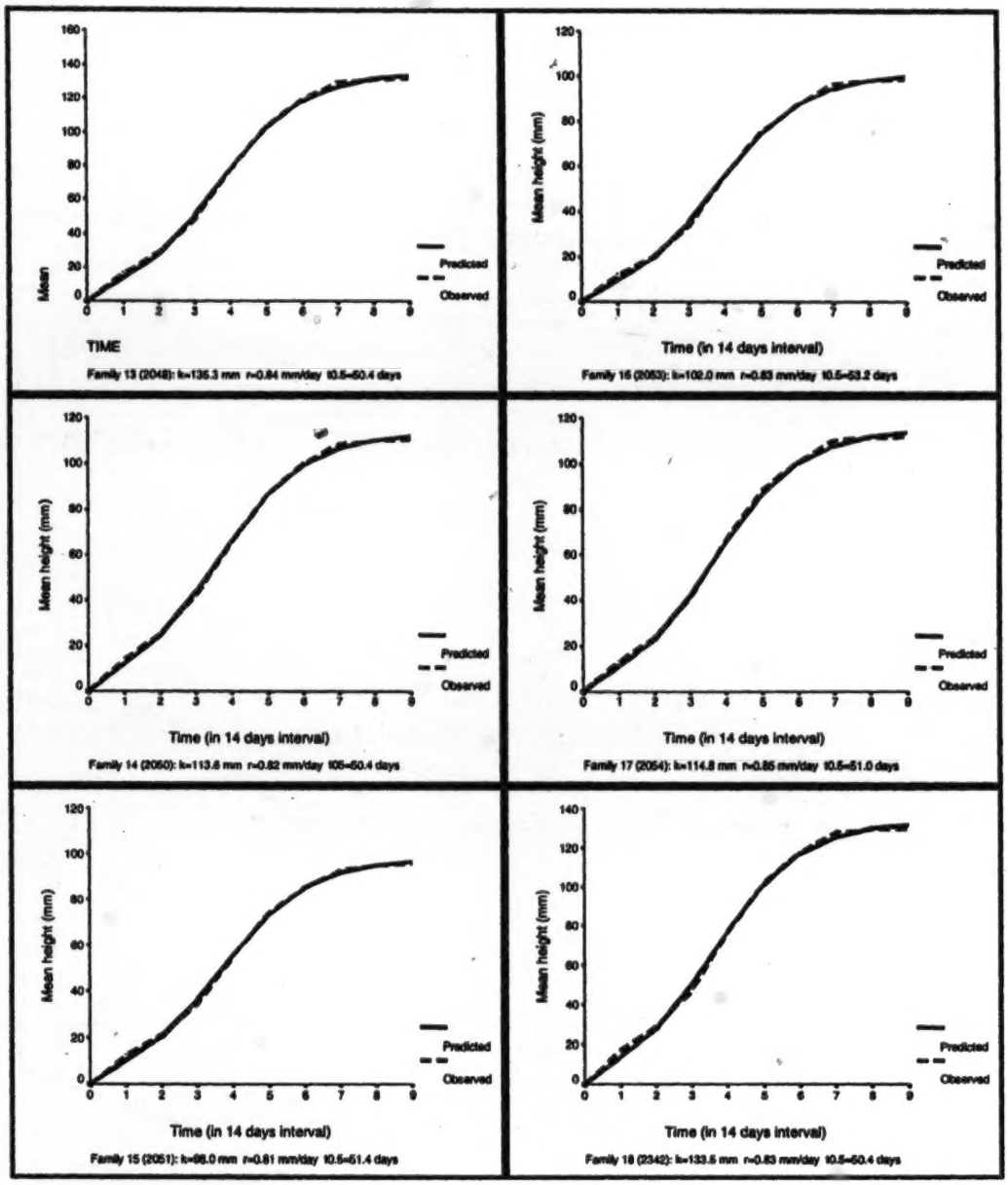
Family	Alberta FS Accession No.	Latitude (N)	Longitude (W)	Elevation (m)
42	2467	55° 42'	119° 22'	884
43	2468	55° 44'	119° 22'	775
44	2469	55° 31'	119° 54'	793
45	2470	55° 33'	119° 54'	793
46	2471	55° 33'	119° 35'	823
47	2472	55° 33'	119° 54'	823
48	2473	55° 34'	119° 53'	832
49	2474	55° 30'	119° 35'	877
50	2476	55° 29'	119° 35'	854
51	2477	55° 35'	119° 56'	793
52	2479	55° 36'	119° 47'	762
53	2480	55° 36'	119° 47'	762
54	2481	55° 36'	119° 48'	762
55	2482	55° 38'	119° 45'	802
56	2483	55° 38'	119° 46'	802
57	2484	55° 28'	119° 35'	823
58	2487	55° 30'	119° 35'	884
59	2488	55° 36'	119° 26'	884
60	2489	55° 27'	119° 37'	884


Mean height (mm)
Time (in 14 days intreval)
Predicted
Observed
Family 1(1926): k=94.0 mm r=0.80 mm/day t0.5=53.4 days
Time (in 14 days interval)
Family 4 (1934): k=126.8 mm r=0.79 mm/day t0.5=50.7 days
Family 2 (1927): k=167.8 mm r=0.78 mm/day t0.5=55.5 days
Family 5 (1936): k=111.6 mm r=0.81 mm/day t0.5=53.5 days
Family 3 (1929): k=133.2 mm r=0.81 mm/day t0.5=51.7 days
Family 6 (1937): k=144.5 mm r=0.87 mm/day t0.5=52.2 days

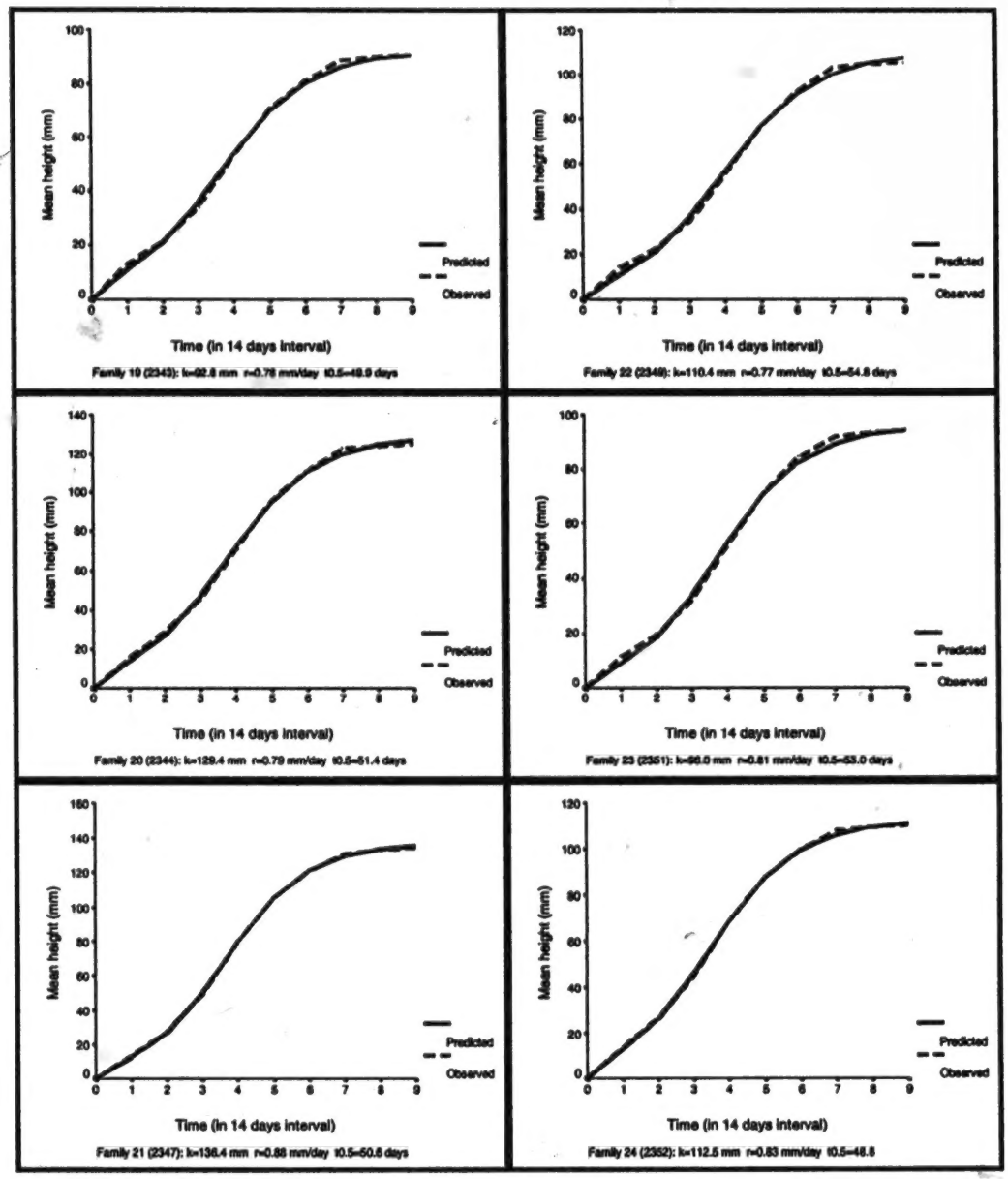
Appendix 2: Observed and predicted family growth curves for the first growth season. The observed curve was generated from the nonlinear regression prediction of cumulative biweekly family mean heights.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 7 (2032): k=120.8 mm r=0.78 mm/day t0.5=53.2 days
Family 10 (2042): k=87.9 mm r=0.76 mm/day t0.5=50.9 days
Family 8 (2034): k=92.2 mm r=0.80 mm/day t0.5=53.4
Family 11 (2046): k=121.3 mm r=0.80 mm/day t0.5=51.1 days
Family 9 (2037): k=105.8 mm r=0.85 mm/day t0.5=49.6 days
Family 12 (2047): k=108.9 mm r=0.79 mm/day t0.5=47.9 days

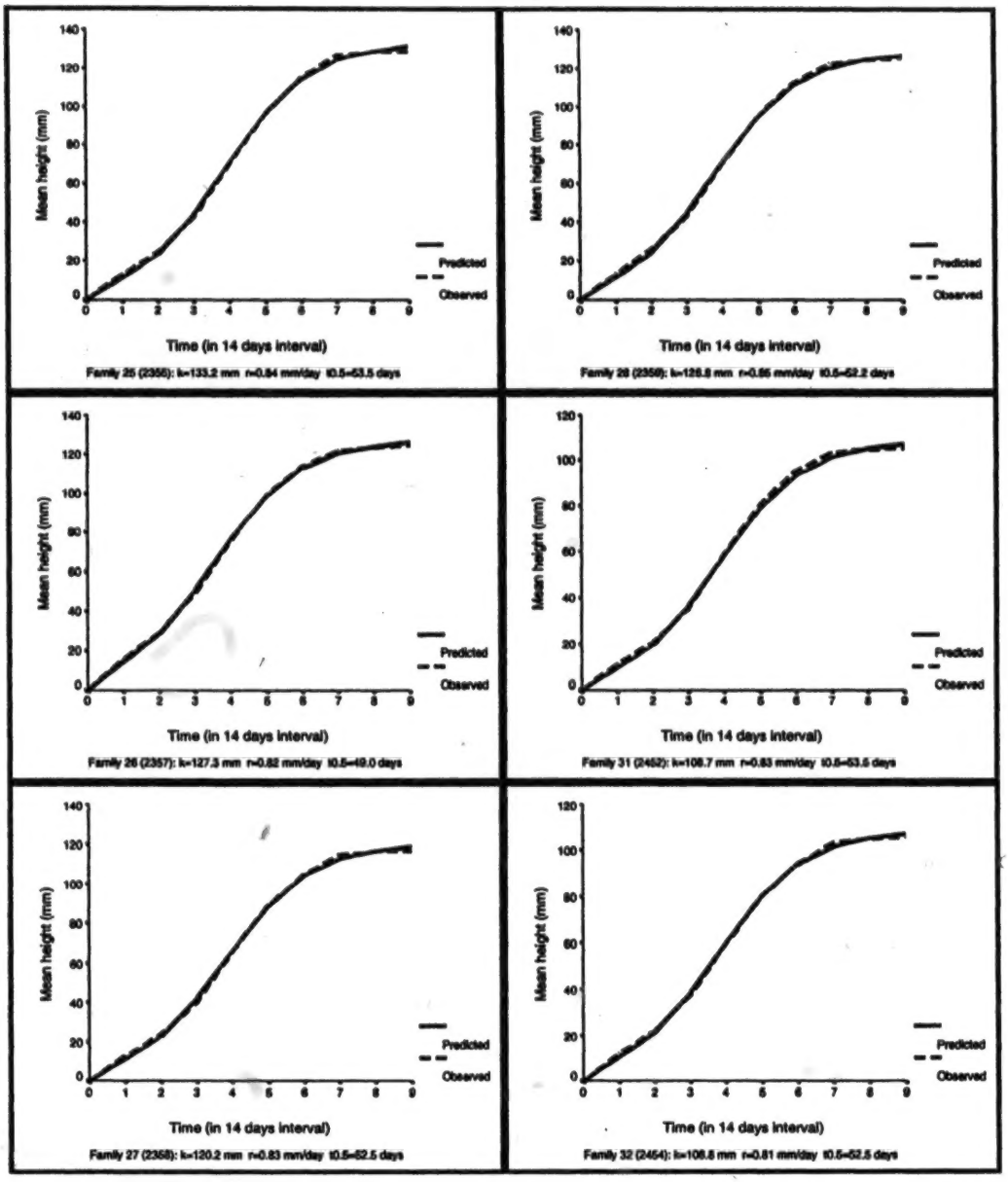
Appendix 2:Continues.


Mean
TIME
Predicted
Observed
Family 13 (2048): k=135.3 mm r=0.84 mm/day t0.5=60.4 days
Mean height (mm)
Time (in 14 days interval)
Family 16 (2053): k=102.0 mm r=0.83 mm/day t0.5=53.2 days
Family 14 (2050): k=113.6 mm r=0.82 mm/day t05=60.4 days
Family 17 (2054): k=114.8 mm r=0.85 mm/day t0.5=51.0 days
Family 15 (2051): k=98.0 mm r=0.81 mm/day t0.5=51.4 days
Family 18 (2342): k=133.5 mm r=0.83 mm/day t0.5=60.4 days

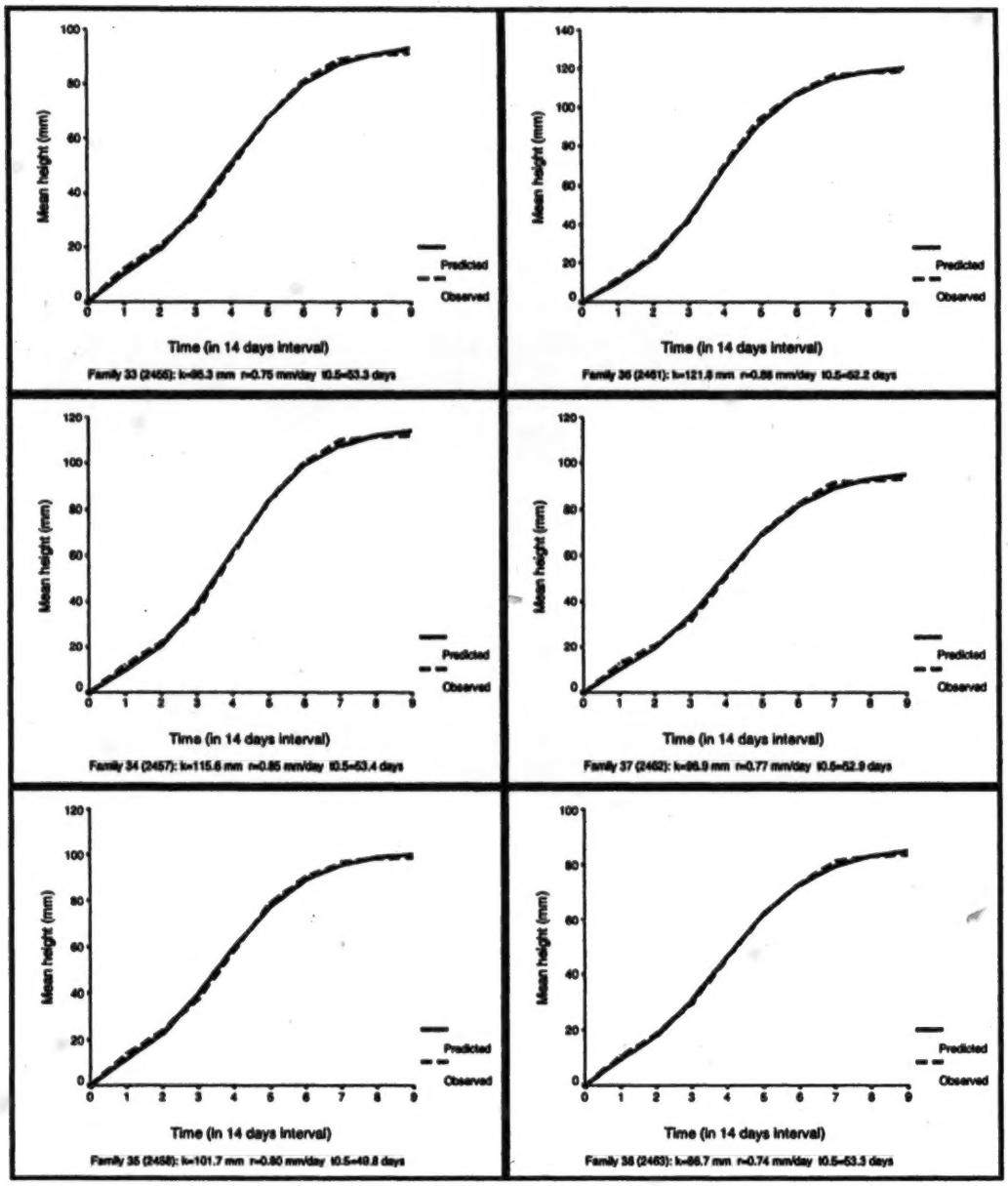
Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 19 (2345): k=92.8 mm r=0.76 mm/day t0.5=48.9 days
Family 22 (2348): k=110.4 mm r=0.77 mm/day t0.5=54.8 days
Family 20 (2344): k=129.4 mm r=0.79 mm/day t0.5=51.4 days
Family 23 (2351): k=98.0 mm r=0.81 mm/day t0.5=53.0 days
Family 21 (2347): k=136.4 mm r=0.88 mm/day t0.5=50.8 days
Family 24 (2352): k=112.5 mm r=0.83 mm/day t0.5=48.8

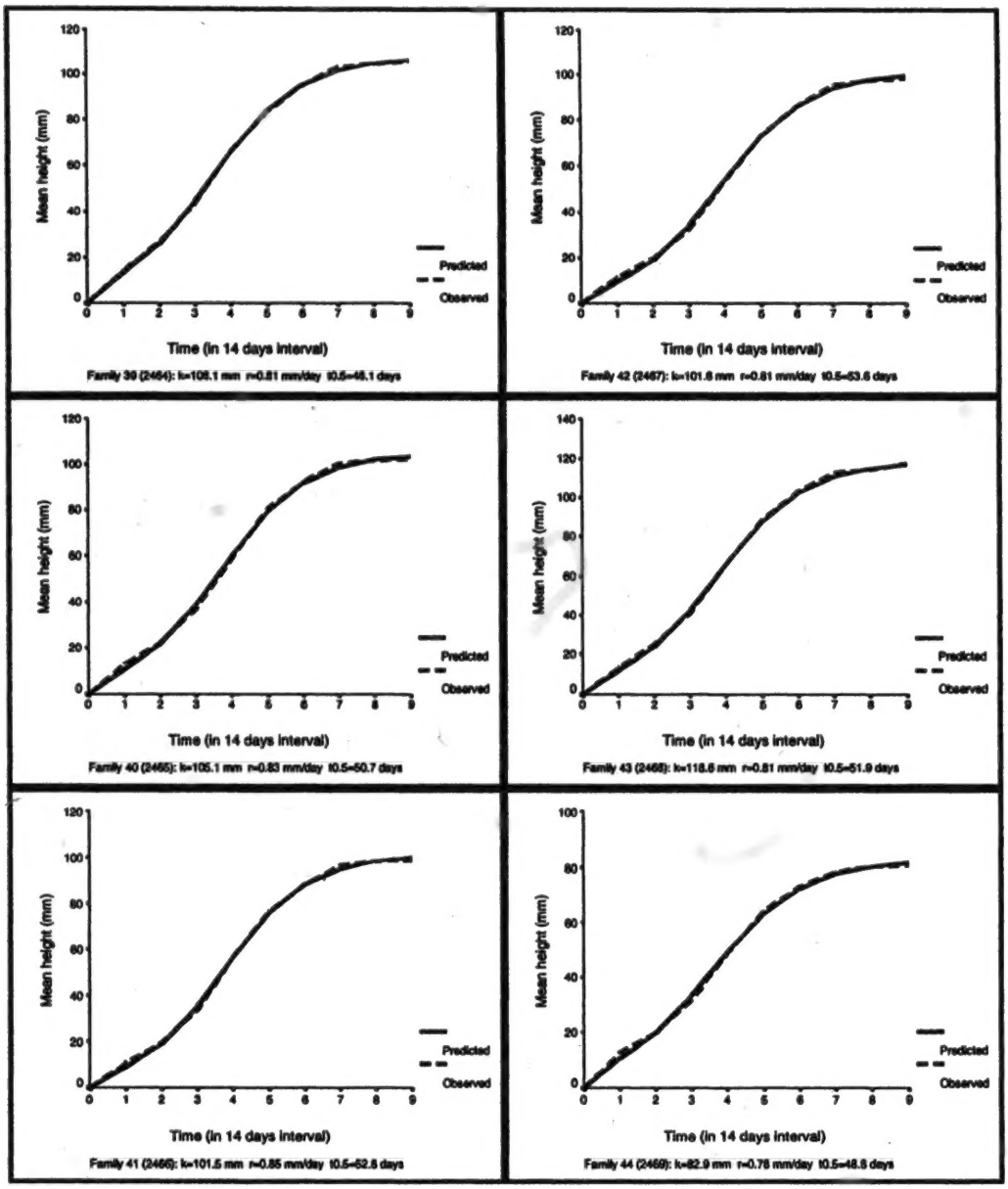
Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 25 (2356): k=133.2 mm r=0.84 mm/day t0.5=53.5 days
Family 28 (2358): k=126.8 mm r=0.85 mm/day t0.5=52.2 days
Family 26 (2357): k=127.3 mm r=0.82 mm/day t0.5=49.0 days
Family 31 (2452): k=108.7 mm r=0.83 mm/day t0.5=53.6 days
Family 27 (2358): k=120.2 mm r=0.83 mm/day t0.5=52.5 days
Family 32 (2454): k=108.8 mm r=0.81 mm/day t0.5=52.5 days

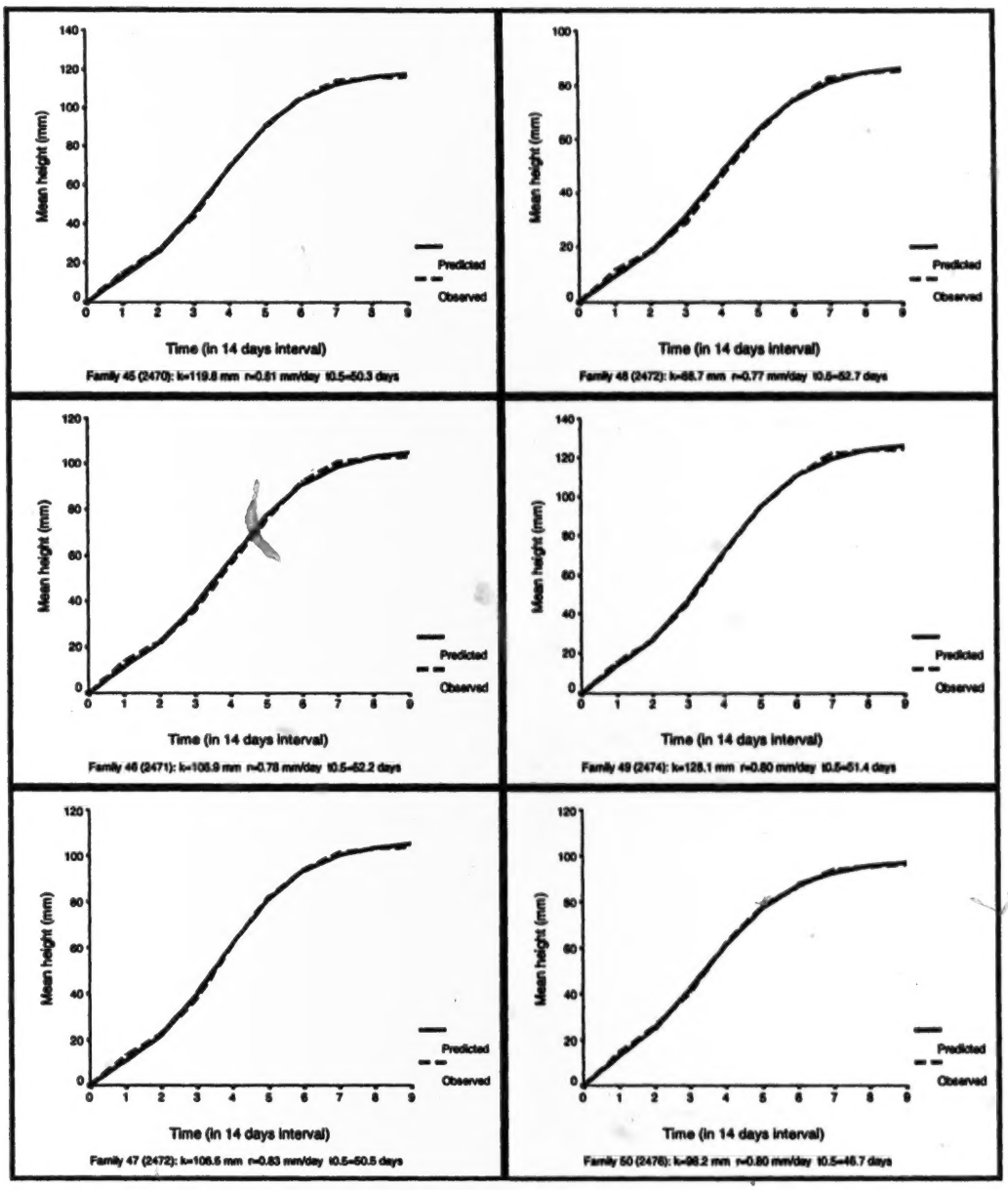
Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 33 (2456): k=96.3 mm r=0.75 mm/day t0.5=53.3 days
Family 36 (2461): k=121.8 mm r=0.86 mm/day t0.5=52.2 days
Family 34 (2457): k=115.6 mm r=0.85 mm/day t0.5=53.4 days
Family 37 (2462): k=96.9 mm r=0.77 mm/day t0.5=52.9 days
Family 35 (2458): k=101.7 mm r=0.80 mm/day t0.5=49.8 days
Family 38 (2463): k=86.7 mm r=0.74 mm/day t0.5=53.3 days

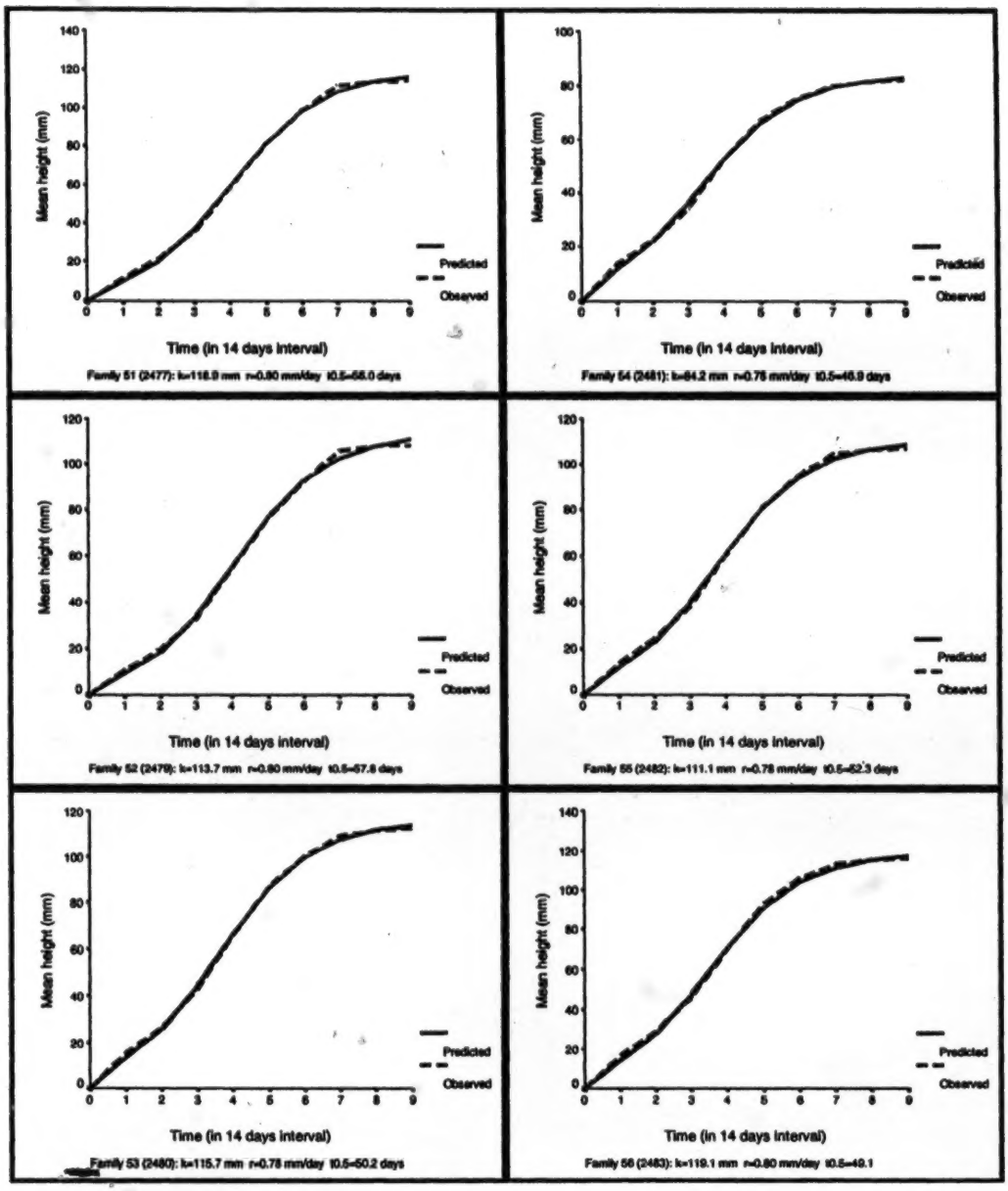
Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 39 (2464): k=108.1 mm r=0.81 mm/day t0.5=46.1 days
Family 42 (2467): k=101.6 mm r=0.81 mm/day t0.5=53.6 days
Family 40 (2465): k=105.1 mm r=0.83 mm/day t0.5=50.7 days
Family 43 (2468): k=118.6 mm r=0.81 mm/day t0.5=51.9 days
Family 41 (2466): k=101.5 mm r=0.85 mm/day t0.5=52.8 days
Family 44 (2469): k=82.9 mm r=0.78 mm/day t0.5=48.8 days

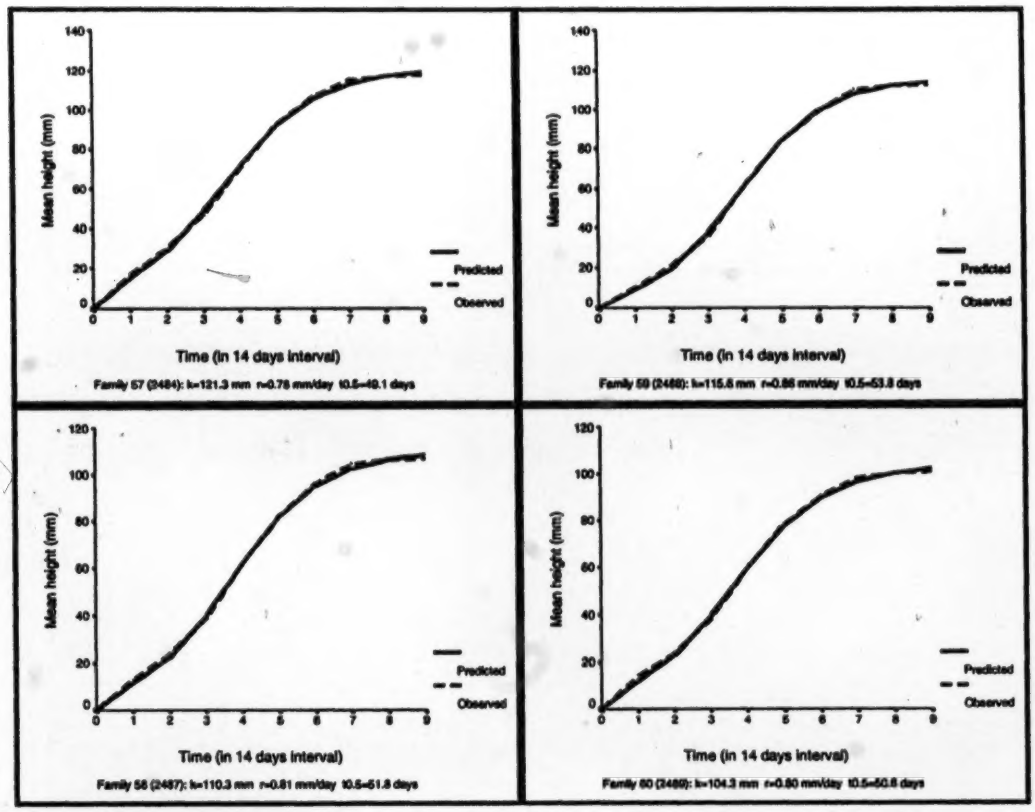
Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 45 (2470): k=119.8 mm r=0.81 mm/day t0.5=50.3 days
Family 48 (2472): k=88.7 mm r=0.77 mm/day t0.5=52.7 days
Family 46 (2471): k=105.9 mm r=0.78 mm/day t0.5=52.2 days
Family 49 (2474): k=128.1 mm r=0.80 mm/day t0.5=51.4 days
Family 47 (2472): k=108.5 mm r=0.83 mm/day t0.5=50.5 days
Family 50 (2476): k=98.2 mm r=0.80 mm/day t0.5=46.7 days

Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 51 (2477): k=118.9 mm r=0.80 mm/day t0.5=55.0 days
Family 54 (2481): k=84.2 mm r=0.76 mm/day t0.5=46.9 days
Family 52 (2479): k=113.7 mm r=0.80 mm/day t0.5=57.6 days
Family 55 (2482): k=111.1 mm r=0.78 mm/day t0.5=52.3 days
Family 53 (2480): k=115.7 mm r=0.78 mm/day t0.5=50.2 days
Family 56 (2483): k=119.1 mm r=0.80 mm/day t0.5=49.1

Appendix 2:Continues.


Mean height (mm)
Time (in 14 days interval)
Predicted
Observed
Family 57 (2484): k=121.3 mm r=0.78 mm/day t0.5=49.1 days
Family 59 (2480): k=115.8 mm r=0.86 mm/day t0.5=53.8 days
Family 58 (2487): k=110.3 mm r=0.81 mm/day t0.5=51.8 days
Family 60 (2480): k=104.3 mm r=0.80 mm/day t0.5=50.8 days

Appendix 2:Continues.

Family	FH18	k_1	k_2	k_3	r_1	r_2	r_3	$t_{0.51}$	$t_{0.52}$	$t_{0.53}$	rFH10	rFH18
2	160.6	170.7	165.2	167.6	0.74	0.74	0.78	56	54.8	55.4	1	1
6	141.0	145.4	142.8	144.5	0.83	0.85	0.87	51.8	50.4	52.2	16	2
21	134.1	136.8	135.5	136.4	0.86	0.86	0.88	50.4	50.4	50.6	26	3
13	131.8	136.1	133.6	135.3	0.80	0.81	0.84	50.4	47.6	50.4	5	4
18	129.7	134.4	131.5	133.5	0.79	0.79	0.83	50.4	50.4	50.7	2	5
3	129.5	134.1	131.6	133.2	0.78	0.78	0.81	51.8	50.4	51.7	12	6
25	129.3	134.5	131.3	133.3	0.80	0.81	0.84	53.2	51.8	53.5	30.5	7
28	125.4	129.8	127.3	128.8	0.81	0.82	0.84	51.8	50.4	52.2	26	8
20	125.1	130.6	127.2	129.4	0.75	0.78	0.79	51.8	49	51.5	75	9
26	124.6	127.6	126.1	127.4	0.80	0.81	0.82	49	47.6	49	6	10
49	124.4	129.1	126.4	128.2	0.77	0.78	0.80	51.8	50.4	51.4	11	11
4	123.1	127.4	125.1	126.8	0.77	0.78	0.79	50.4	49	50.7	10	12
36	121.8	125.1	123.2	124.5	0.87	0.87	0.89	51.8	50.4	51.6	46.5	13
57	117.8	121.8	119.5	121.3	0.75	0.77	0.78	49	47.6	49.1	4	14
11	117.5	122.2	119.7	121.3	0.77	0.78	0.80	51.8	50.4	51.1	14.5	15
43	117.4	121.1	119.1	120.3	0.79	0.80	0.82	51.8	50.4	52	26	16
7	116.5	122.5	118.8	120.8	0.73	0.75	0.78	53.2	51.8	53.2	18	17
45	116.3	120.2	118.2	119.5	0.78	0.77	0.81	50.4	49	50.2	13	18
27	116.2	120.3	118.1	119.5	0.79	0.80	0.82	51.8	50.4	52.6	34	19

Appendix 3: Family means for final first season height, growth curve parameters, and ranking of families for initial (rFH2) and final (rFH18) observed height. Subscripts 1, 2, and 3 on r and $t_{0.5}$ stand for method of sums of reciprocals, method of selected points and nonlinear regression, respectively.

Family	FH18	k_1	k_2	k_3	r_1	r_2	r_3	$t_{0.51}$	$t_{0.52}$	$t_{0.53}$	rFH10	rFH18
56	115.9	119.7	117.4	119.1	0.77	0.79	0.80	49	46.2	49.1	3	20
51	114.1	121.1	116.9	118.9	0.75	0.77	0.80	57.4	54.6	56	46.5	21
17	113.8	117.5	115.3	116.7	0.81	0.82	0.85	50.4	49	51.1	30.5	22
53	112.4	116.7	114.4	115.7	0.75	0.76	0.78	50.4	47.6	40.2	9	23.5
59	112.4	116.4	114.0	115.4	0.83	0.85	0.81	54.6	51.8	53.7	58	23.5
34	111.7	116.4	113.7	115.3	0.80	0.81	0.85	53.2	51.8	53.4	46.5	25
14	110.4	114.2	112.0	113.6	0.79	0.80	0.82	50.4	47.6	50.4	18	26
24	110.1	113.4	111.7	112.5	0.81	0.82	0.83	49	47.6	48.1	18	27
52	108.6	119.6	113.7	113.7	0.74	0.76	0.80	61.8	58.8	57.9	57	28
5	108.2	112.8	109.9	111.6	0.75	0.78	0.81	53.2	50.4	53.5	38	29
31	107.4	112.1	109.3	110.8	0.79	0.80	0.83	53.2	51.8	53.5	49.5	30
58	107.2	110.8	109.0	110.3	0.79	0.79	0.81	51.8	50.4	51.8	36	31
55	107.1	112.9	109.3	111.1	0.74	0.76	0.78	53.2	50.4	52.4	26	32
12	106.2	109.2	107.6	108.9	0.77	0.79	0.79	47.6	46.2	47.9	7.5	33
39	105.9	108.6	107.4	108.9	0.80	0.80	0.81	47.6	47.6	48.1	20	34
32	105.7	110.2	107.6	108.9	0.77	0.78	0.81	53.2	51.8	52.5	41.5	35
22	105.4	113.8	108.7	110.4	0.70	0.71	0.77	56	51.8	54.8	22	36
9	104.1	106.9	105.3	106.1	0.83	0.84	0.86	49	49	49.8	41.5	37.5
47	104.1	106.9	105.5	106.5	0.80	0.81	0.83	50.4	49	50.5	34	37.5

Appendix 3: Continues.

Family	FH18	k_1	k_2	k_3	r_1	r_2	r_3	$t_{0.51}$	$t_{0.52}$	$t_{0.53}$	rFH10	rFH18
46	103.3	108.2	105.3	106.9	0.74	0.74	0.78	51.8	50.4	52.3	26	39
40	102.3	105.6	103.5	105.1	0.80	0.81	0.83	50.4	47.6	50.7	34	40
60	101.3	105.2	103.2	104.4	0.77	0.77	0.80	50.4	49	50.6	21	41
35	99.2	102.7	100.5	102.1	0.77	0.80	0.80	50.4	47.6	53.9	29	42
41	98.6	102.2	100.2	101.2	0.81	0.82	0.85	53.2	50.4	52.6	56	43
42	98.4	103.1	100.4	101.6	0.75	0.77	0.81	53.2	57.8	53.6	53	44
16	97.4	102.2	99.5	100.5	0.77	0.78	0.83	53.2	51.8	53.2	49.5	45
50	96.3	98.5	97.5	98.2	0.79	0.80	0.80	46.2	44.2	46.7	14.5	46
15	95.7	98.8	97.2	98.2	0.77	0.78	0.81	51.8	49	51.4	41.5	47
23	94.2	98.5	96.0	96.1	0.76	0.78	0.81	53.2	50.4	52.9	51.5	48
37	93.4	98.5	95.5	97.1	0.71	0.73	0.77	53.2	50.4	53.8	41.5	49
33	91.6	96.8	94.0	95.3	0.71	0.72	0.75	54.6	51.8	53.3	44	50
1	90.9	95.9	93.3	94.0	0.75	0.75	0.80	54.6	50.4	53.4	46.5	51
19	90.6	94.2	92.3	93.6	0.74	0.76	0.78	50.4	47.6	50.1	32	52
8	88.7	93.3	90.9	92.2	0.73	0.73	0.77	53.2	50.4	53.4	53.5	53
10	85.6	88.9	87.5	88.2	0.73	0.74	0.76	50.4	47.6	50.5	38	54.5
48	85.6	89.8	89.0	88.7	0.73	0.72	0.77	53.2	51.8	52.7	51.5	54.5
38	82.1	86.5	84.3	85.3	0.70	0.71	0.73	53.2	51.8	53.3	55	56
54	82.0	84.1	83.1	84.0	0.77	0.77	0.78	46.2	43.4	46.9	23	57
44	80.6	83.3	81.8	82.9	0.74	0.76	0.78	47.6	44.8	48.8	38	58

Appendix 3: Continues.

Family	SH18	k_1	k_2	k_3	r_1	r_2	r_3	$t_{0.51}$	$t_{0.52}$	$t_{0.53}$	rSH2	rSH18
2	168.1	191.6	182.0	182.9	0.68	0.62	0.67	57.4	54.6	55.9	1	1
8	153.7	188.4	174.3	186.8	0.53	0.52	0.59	65.8	63	64.4	9	2
20	134.1	168.1	152.9	182.9	0.59	0.55	0.58	64.4	60.2	63	8	3
6	126.3	153.3	152.5	158.3	0.51	0.50	0.55	60.2	61.6	57.1	3	4
3	125.9	165.0	151.0	148.6	0.47	0.48	0.50	75.6	68.6	66.8	23	5
7	122.9	187.3	160.0	144.4	0.48	0.46	0.54	75.6	70	60.2	4	6
22	116.9	146.5	137.3	136.9	0.48	0.45	0.52	64.4	60.2	62.3	2	7
28	116.8	152.1	133.2	134.6	0.48	0.49	0.54	68.6	60.2	60.9	29.5	8
38	115.1	131.4	127.9	NA	0.53	0.50	NA	NA	NA	NA	43	9
27	114.7	151.3	131.8	134.7	0.50	0.52	0.58	64.4	58.8	56.5	19.5	10
37	114.3	137.8	128.9	129.7	0.56	0.56	0.56	60.2	56	56	7	11
9	111.2	162.6	137.7	142.6	0.42	0.42	0.48	78.4	71.4	69.1	26	12
60	108.8	152.3	143.5	141.3	0.50	0.46	0.54	70	71.4	67.6	31	13
34	108.4	135.6	131.1	134.7	0.49	0.46	0.53	70	71.4	65.4	42	14
46	105.6	138.0	122.0	119.3	0.50	0.49	0.53	67.2	63	60.5	41	15
36	105.3	127.1	117.0	119.3	0.49	0.52	0.53	57.4	50.4	52.5	24	16
45	105.2	132.3	116.8	132.8	0.51	0.47	0.52	65.8	60.2	58.7	19.5	17
59	105.2	140.2	123.8	127.1	0.40	0.42	0.46	74.2	61.6	67.4	15	18
32	103.0	138.0	121.3	116.2	0.49	0.51	0.55	67.2	60.2	56.4	22	19

Appendix 4: Family means for final second season height, growth curve parameters, and ranking of families for initial (rSH2) and final (rSH18) observed height. Subscripts 1, 2, and 3 on r and $t_{0.5}$ stand for method of sums of reciprocals, method of selected points and nonlinear regression, respectively.

Family	SH18	k_1	k_2	k_3	r_1	r_2	r_3	$t_{0.51}$	$t_{0.52}$	$t_{0.53}$	rSH2	rSH18
42	102.9	130.0	118.1	111.0	0.47	0.49	0.50	60.2	56	53.5	5	20
39	102.3	127.8	121.4	129.6	0.46	0.42	0.49	60.2	60.2	59.3	10	21
57	102.1	154.5	128.6	135.6	0.39	0.39	0.44	79.8	67.2	64.6	12	22
21	101.9	124.0	115.2	123.3	0.57	0.57	0.55	63	58.8	61.3	29.5	23
53	101.8	129.8	115.2	120.3	0.55	0.54	0.59	63	57.4	55.4	25	24
13	100.4	129.6	120.2	116.1	0.56	0.48	0.56	60.2	61.6	55.1	6	25
18	98.4	146.6	117.3	114.0	0.49	0.51	0.54	72.8	61.6	58.7	21	26
43	97.7	122.3	112.9	114.7	0.48	0.48	0.51	65.8	61.6	62.7	28	27
31	97.3	121.8	111.0	116.3	0.50	0.53	0.52	61.6	54.6	58.5	11	28
12	96.0	114.5	106.1	110.7	0.53	0.54	0.54	56	50.4	54	18	29
51	95.2	125.8	115.7	111.5	0.48	0.48	0.54	63	60.2	57.2	34	30
56	93.5	114.7	107.5	105.0	0.42	0.43	0.44	58.8	54.6	57.3	14	31
4	93.0	139.0	126.8	122.5	0.49	0.45	0.53	74.2	74.2	67.9	44	32
24	92.8	119.4	108.5	107.7	0.58	0.51	0.54	63	57.4	58.7	13	33
49	92.2	107.4	106.0	101.8	0.63	0.54	0.61	53.2	53.2	52.2	16	34
41	90.5	111.9	104.4	111.6	0.45	0.48	0.51	64.4	58.8	59	33	35
1	88.7	117.8	108.4	113.7	0.49	0.46	0.51	65.8	56	55.4	37.5	36
11	88.5	105.2	97.7	105.8	0.46	0.46	0.51	58.8	51.8	52.3	27	37
33	87.6	116.9	106.5	123.6	0.51	0.53	0.51	71.4	67.2	73.4	51	38

Appendix 4: Continues.

Family	SH18	K_1	k_2	k_3	r_1	r_2	r_3	$t_{0.51}$	$t_{0.52}$	$t_{0.53}$	rSH10	rSH18
5	86.5	112.9	113.1	105.2	0.53	0.48	0.49	61.6	61.6	60.8	45	39
25	86.5	113.6	100.0	111.5	0.55	0.57	0.52	61.6	53.2	59.3	35	40
17	85.5	95.8	97.1	99.5	0.58	0.50	0.59	53.2	54.6	50.1	17	41
14	82.2	116.6	102.8	116.9	0.44	0.40	0.47	72.8	63	64.5	39	42
26	80.4	96.9	92.2	94.6	0.52	0.48	0.51	56	54.6	53.4	32	43
52	80.0	107.5	92.3	104.1	0.46	0.45	0.49	64.4	54.6	58.3	37.5	44
35	78.0	91.6	88.6	97.6	0.54	0.52	0.54	50.4	46.2	53.2	36	45
16	77.8	101.7	89.8	90.3	0.46	0.47	0.49	57.4	51.8	50.8	40	46
48	74.4	94.5	87.6	88.8	0.48	0.47	0.50	65.8	63	62.2	49	47
55	73.2	98.8	91.8	93.4	0.47	0.46	0.49	65.8	64.4	60.5	48	48
44	70.9	108.6	95.6	96.4	0.41	0.42	0.47	77	70	67.2	50	49
19	70.2	89.4	82.5	82.0	0.54	0.53	0.51	60.2	58.8	56.3	56	50
15	66.6	90.6	85.5	89.3	0.43	0.42	0.44	67.2	67.2	66	54	51
23	66.3	79.3	78.5	86.3	0.50	0.50	0.52	56	54.6	55.4	55	52
47	62.9	76.6	70.7	81.0	0.46	0.49	0.51	53.2	49	47.9	46	53
50	62.1	74.3	71.5	77.6	0.47	0.46	0.50	58.8	57.4	57.4	53	54
58	60.5	98.4	75.8	94.5	0.50	0.52	0.45	60.2	54.6	66.6	52	55
10	54.3	66.3	59.0	74.5	0.54	0.57	0.56	51.8	42	49.2	57	56
40	48.4	57.1	52.3	66.2	0.52	0.52	0.48	43.4	44.8	42.8	47	57
54	42.6	51.3	46.7	74.0	0.47	0.50	0.50	61.6	54.6	65	58	58

Appendix 4:Continues.

Family	TH36	D23	D3	BL	NL	NBR	NBD	SL	NSU	MSUL	TB2	BB2
2	320.5	5.52	8.39	124.5	14.7	18.7	8.8	93.9	270.1	0.343	7.9	7.4
20	253.5	5.03	8.78	95.6	13.9	18.1	8.0	78.1	241.3	0.318	7.8	7.3
3	249.8	3.93	7.70	108.0	12.9	15.8	6.6	89.0	253.5	0.348	7.2	7.0
6	246.8	3.74	6.07	96.8	12.5	16.8	8.0	77.3	217.3	0.348	5.9	5.9
28	240.8	4.40	7.61	102.7	11.4	16.4	7.2	89.0	268.2	0.331	8.7	8.3
8	238.6	3.93	7.30	86.0	12.8	12.4	6.3	77.0	246.5	0.309	6.9	6.8
21	237.3	3.80	6.46	100.0	11.5	18.3	8.9	74.8	228.7	0.329	6.6	6.5
7	233.8	4.87	7.58	101.9	13.0	16.7	7.5	78.7	237.2	0.327	9.6	9.0
27	226.6	3.76	7.33	84.9	12.3	14.5	6.5	76.5	234.7	0.321	7.9	7.7
13	224.9	4.31	6.10	91.0	13.5	17.0	8.2	61.9	217.0	0.284	9.8	9.3
25	218.7	3.69	6.70	112.3	11.9	16.3	7.14	82.9	233.9	0.354	7.2	7.0
49	218.7	4.75	8.04	98.8	12.7	17.8	7.5	91.5	258.1	0.354	7.8	7.5
34	217.2	3.94	5.80	90.4	11.3	15.3	6.8	73.2	233.8	0.309	6.6	6.5
18	215.9	3.86	6.84	104.2	13.0	15.0	7.0	86.8	249.2	0.346	7.1	6.9
22	215.3	3.60	6.48	84.1	12.0	13.1	5.4	69.7	223.8	0.312	7.5	7.1
4	214.1	3.78	6.27	104.3	12.2	16.2	7.1	89.7	241.8	0.368	6.7	6.6
9	213.8	3.86	6.92	84.8	11.5	15.5	6.4	68.1	232.0	0.295	8.6	8.4
45	209.6	4.14	7.53	97.3	12.7	16.1	7.2	80.6	238.9	0.328	8.9	8.4
59	208.8	3.82	6.51	88.0	11.6	13.0	6.0	69.4	224.0	0.315	7.3	7.0

Appendix 5: Family means for traits other than those involved in growth curve analysis arranged in the descending order for TH36.

Family	TH36	D23	D3	BL	NL	NBR	NBD	SL	NSU	MSUL	TB2	BB2
43	208.4	4.16	7.73	103.8	11.3	15.2	6.6	86.0	277.1	0.308	6.7	6.6
32	207.3	3.73	6.83	90.5	11.5	13.4	5.6	93.2	264.5	0.354	8.4	8.3
51	206.4	3.97	5.83	109.1	13.1	14.7	7.8	81.8	241.1	0.334	7.5	7.3
57	205.8	4.07	8.95	105.5	12.2	17.5	7.8	84.3	263.2	0.322	6.6	6.5
26	205.4	4.00	6.69	100.1	11.8	16.9	6.9	81.4	248.4	0.325	7.2	7.0
53	204.9	4.12	7.88	99.0	12.6	15.7	6.5	86.5	271.3	0.316	9.2	8.9
36	204.3	3.36	6.53	93.5	12.1	13.0	5.0	87.7	260.1	0.330	7.8	7.8
39	202.3	3.85	7.30	83.0	10.9	15.0	7.3	72.7	210.5	0.346	7.3	7.1
11	202.2	3.72	7.22	100.0	11.7	14.7	6.2	73.8	237.9	0.315	7.5	7.4
38	199.9	NA	NA	86.2	11.6	11.5	4.9	82.2	241.7	0.334	NA	NA
60	199.5	3.86	6.80	80.1	12.9	13.2	5.4	67.8	251.7	0.275	8.2	8.1
37	199.2	4.23	7.94	81.6	12.5	14.1	5.1	69.4	262.5	0.261	8.3	8.1
17	199.1	4.34	7.82	98.2	12.4	14.3	5.8	74.4	227.4	0.324	7.5	7.4
56	199.0	3.27	5.91	87.8	13.5	12.9	5.6	91.2	240.6	0.574	7.5	7.5
31	197.4	3.66	5.68	96.4	12.8	13.2	5.3	67.4	235.5	0.284	7.3	7.2
46	196.3	3.76	6.67	80.2	12.7	13.5	6.7	66.1	224.5	0.293	8.0	7.9
24	194.0	4.07	7.14	81.2	12.1	16.8	7.8	59.9	219.8	0.272	7.4	7.3
12	193.7	4.41	8.50	71.3	11.9	17.0	8.8	68.1	234.4	0.287	7.3	7.0
42	192.8	3.62	5.96	88.6	12.2	12.7	5.7	73.1	241.3	0.302	7.1	7.0

Appendix 5: Continues.

Family	TH36	D23	D3	BL	NL	NBR	NBD	SL	NSU	MSUL	TB2	BB2
14	192.0	3.12	5.10	94.1	12.0	11.1	5.2	80.0	235.6	0.328	8.4	8.2
41	184.6	2.31	4.32	67.3	11.8	9.8	2.6	64.4	216.4	0.300	7.5	7.3
5	183.9	2.90	5.85	79.3	11.7	14.6	5.1	64.4	200.6	0.318	7.9	7.9
55	182.5	3.31	6.30	89.7	12.8	13.3	5.0	72.6	238.8	0.304	7.3	7.2
52	181.0	3.24	5.36	87.8	12.9	11.1	5.5	70.3	202.3	0.340	7.4	7.3
33	176.9	3.59	6.94	86.5	12.3	11.3	4.4	75.7	235.0	0.320	7.0	6.8
35	171.0	3.61	5.96	70.3	12.9	12.5	6.1	64.9	218.7	0.291	8.2	8.1
58	167.8	2.86	4.73	77.2	10.3	13.4	6.5	68.5	210.8	0.328	7.6	7.5
47	167.0	2.93	4.55	80.2	11.1	13.0	5.5	NA	NA	NA	7.4	7.4
23	165.4	2.94	6.01	61.2	11.4	11.4	4.4	51.9	192.1	0.271	8.4	8.2
1	164.6	3.12	5.55	76.7	12.8	10.1	3.3	74.1	220.1	0.327	7.1	7.0
16	163.1	2.50	4.53	67.0	11.6	10.4	3.4	NA	NA	NA	8.2	8.1
48	161.1	2.91	5.08	81.3	11.6	10.6	4.4	67.7	220.9	0.302	7.6	7.4
15	160.9	2.49	5.59	72.6	12.3	10.4	4.2	68.6	243.2	0.282	7.9	7.7
50	153.4	3.22	5.68	59.6	10.7	14.1	7.0	NA	NA	NA	8.8	8.4
19	145.1	3.44	6.86	73.4	11.0	12.9	5.3	71.4	231.5	0.309	8.6	8.3
40	141.7	2.91	4.43	74.6	11.0	14.0	6.4	NA	NA	NA	7.4	7.3
10	139.2	2.52	5.39	67.8	10.9	12.9	4.0	NA	NA	NA	7.0	7.0
44	138.4	2.68	5.17	66.3	11.2	12.2	5.9	54.3	182.7	0.299	7.2	7.2
54	123.6	2.36	5.35	51.7	11.0	11.6	5.0	50.2	183.7	0.268	7.5	7.5

Appendix 5: Continues.

Family	BB3	FB	FS	FR	DB	DS	DR	RSR	AH10	AH11	BH10	BH11
2	8.9	40.2	17.9	16.9	19.9	9.0	13.1	0.425	115.5	132.4	120.8	157.9
20	10.2	30.0	16.1	13.5	14.8	7.7	9.9	0.411	83.7	97.4	103.5	135.0
3	8.7	31.5	14.9	13.5	15.4	7.6	9.8	0.368	78.8	92.7	136.1	177.8
6	8.1	20.0	10.6	9.7	9.9	5.5	6.3	0.336	NA	NA	NA	NA
28	10.0	32.6	18.4	13.9	15.0	9.6	10.9	0.442	75.2	89.9	123.8	156.9
8	8.8	25.9	15.3	11.9	12.2	7.7	9.6	0.446	83.4	96.8	117.8	151.6
21	8.7	21.0	11.2	8.0	9.4	5.1	5.9	0.379	85.3	100.0	117.0	156.2
7	9.6	24.3	14.1	10.4	11.3	6.7	7.3	0.392	73.8	88.3	121.1	156.1
27	10.1	28.3	14.6	16.8	13.6	7.4	9.5	0.472	80.9	92.5	126.2	160.8
13	8.9	36.2	14.6	14.9	17.8	7.8	10.5	0.360	93.6	106.7	126.3	166.7
25	8.8	20.4	10.9	6.7	9.1	5.2	5.4	0.353	91.2	105.6	130.1	165.0
49	9.5	32.1	14.6	14.1	15.1	7.3	8.7	0.347	91.5	104.6	117.9	150.8
34	8.8	30.1	13.5	12.7	14.0	7.3	10.3	0.422	90.1	103.9	119.4	158.1
18	9.1	25.5	11.7	8.7	11.2	5.7	6.0	0.282	105.6	123.0	132.9	164.7
22	9.1	21.8	11.4	8.4	10.6	5.8	6.4	0.357	90.1	104.0	134.1	173.9
4	9.4	22.5	9.2	6.7	9.5	4.7	5.4	0.328	101.6	122.1	132.8	171.9
9	9.4	19.6	9.8	7.6	9.3	4.9	5.7	0.356	85.9	100.8	117.1	151.8
45	10.4	21.4	11.6	10.1	9.9	5.8	7.7	0.490	83.6	97.6	132.7	169.9
59	9.0	23.0	12.1	9.6	11.1	6.4	7.9	0.394	70.2	80.9	114.1	148.3

Appendix 5: Continues.

Family	BB3	FB	FS	FR	DB	DS	DR	RSR	AH10	AH11	BH10	BH11
43	9.0	26.1	11.8	11.5	12.2	6.1	8.0	0.393	84.0	98.4	113.1	143.1
32	10.2	23.3	12.9	11.2	11.5	6.6	8.7	0.416	88.8	106.9	131.7	171.9
51	9.3	20.3	11.2	7.9	9.1	5.0	5.8	0.357	93.2	107.2	138.9	183.8
57	8.9	29.3	14.8	12.3	14.5	7.6	9.2	0.396	66.9	77.3	89.1	117.1
26	8.9	31.2	15.4	18.2	16.4	8.9	13.7	0.503	118.1	137.8	118.7	155.4
53	10.1	28.5	12.0	11.4	13.1	6.0	9.0	0.417	97.2	114.6	123.5	161.6
36	8.8	23.2	12.6	7.4	10.6	5.8	5.7	0.327	94.0	108.7	126.9	162.8
39	8.7	21.1	12.9	8.6	10.2	6.4	6.8	0.357	90.3	107.8	131.0	167.0
11	10.7	26.5	11.5	12.5	12.3	5.9	8.2	0.391	82.5	95.7	126.2	160.9
38	NA	NA	NA	NA	NA	NA	NA	NA	78.6	92.1	120.1	157.7
60	8.7	18.1	12.6	9.7	9.0	6.7	7.2	0.424	86.4	100.7	108.9	144.9
37	10.2	33.1	13.7	16.4	15.2	7.0	11.0	0.501	91.0	105.9	112.8	151.0
17	8.9	24.4	12.4	13.4	11.2	6.3	9.6	0.503	70.8	84.7	140.7	182.8
56	9.4	17.9	9.1	7.9	8.3	4.7	5.0	0.336	91.3	107.3	119.3	151.4
31	8.9	NA	NA	NA	NA	NA	NA	NA	90.7	102.8	144.9	183.9
46	9.5	23.2	11.9	9.3	10.6	5.7	7.0	0.416	64.3	74.8	110.7	142.1
24	8.4	21.9	11.5	10.0	10.3	5.7	7.0	0.414	73.4	85.2	107.3	143.7
12	8.8	28.4	17.0	14.3	13.8	8.6	11.0	0.466	92.1	109.4	116.0	152.0
42	9.5	24.0	11.8	9.8	11.3	5.9	6.7	0.372	97.2	113.0	114.8	150.5

Appendix 5: Continues.

Family	BB3	FB	FS	FR	DB	DS	DR	RSR	AH10	AH11	BH10	BH11
14	9.3	15.3	7.3	4.7	7.0	3.7	3.4	0.313	77.7	97.5	123.4	161.0
41	9.6	NA	NA	NA	NA	NA	NA	NA	86.3	101.8	118.4	152.9
5	9.2	15.1	7.8	5.6	6.4	3.3	4.0	0.365	101.1	116.8	130.8	169.7
55	8.7	29.9	13.6	10.0	13.4	6.7	7.6	0.318	97.6	112.1	134.3	171.3
52	8.7	11.9	8.1	5.7	5.3	3.7	4.5	0.439	98.4	114.6	132.2	175.4
33	9.0	22.1	10.4	10.7	10.0	5.3	7.5	0.456	78.2	91.2	121.9	158.0
35	8.2	21.7	11.1	10.6	10.0	5.3	7.1	0.440	84.3	99.3	118.9	154.4
58	8.8	NA	NA	NA	NA	NA	NA	NA	82.0	97.1	118.9	150.2
47	9.3	NA	NA	NA	NA	NA	NA	NA	79.3	93.7	114.1	145.7
23	9.7	15.7	10.7	6.7	6.5	5.4	4.8	0.361	91.0	105.6	123.1	158.7
1	9.1	17.8	11.2	5.7	7.7	5.0	4.4	0.260	106.7	122.9	123.7	163.1
16	8.9	NA	NA	NA	NA	NA	NA	NA	81.7	92.7	133.3	170.1
48	8.8	15.0	9.7	5.8	6.8	4.9	4.4	0.380	80.5	94.5	118.1	153.2
15	9.9	16.6	8.4	7.3	7.7	4.6	5.7	0.398	88.2	105.3	119.4	152.3
50	9.6	14.0	8.7	4.9	6.0	3.7	3.5	0.321	92.9	107.3	124.8	166.2
19	8.3	20.1	10.8	7.7	9.0	5.0	5.6	0.386	79.2	92.4	94.8	126.6
40	8.9	NA	NA	NA	NA	NA	NA	NA	83.6	101.0	111.2	143.3
10	8.7	NA	NA	NA	NA	NA	NA	NA	99.7	113.8	135.7	175.7
44	8.8	NA	NA	NA	NA	NA	NA	NA	79.8	93.9	118.5	154.9
54	9.4	NA	NA	NA	NA	NA	NA	NA	82.1	98.8	106.8	144.7

Appendix 5: Continues.

Family	HI	BI	ST	ST*	CS
2	0.30	0.44	0.018	57.1	0.34
20	0.35	0.55	0.021	48.4	0.36
3	0.34	0.54	0.017	63.1	0.48
6	0.35	0.55	0.017	63.3	0.35
28	0.39	0.71	0.017	61.6	0.44
8	0.38	0.63	0.019	52.7	0.50
21	0.31	0.45	0.018	57.7	0.45
7	0.34	0.53	0.021	48.1	0.40
27	0.38	0.64	0.018	59.0	0.45
13	0.30	0.45	0.018	119.0	0.41
25	0.34	0.54	0.019	53.5	0.47
49	0.32	0.51	0.020	45.5	0.40
34	0.34	0.52	0.020	50.3	0.42
18	0.36	0.60	0.020	53.2	0.44
22	0.40	0.80	0.019	55.9	0.46
4	0.33	0.59	0.017	60.9	0.43
9	0.34	0.53	0.020	51.9	0.51
45	0.37	0.59	0.021	50.7	0.37
59	0.37	0.65	0.020	53.2	0.44
43	0.32	0.50	0.020	47.7	0.49
32	0.34	0.52	0.020	52.1	0.53
51	0.37	0.62	0.020	54.1	0.48
57	0.33	0.49	0.020	51.3	0.46
26	0.36	0.59	0.020	51.8	0.48
53	0.31	0.46	0.019	51.9	0.49
36	0.35	0.60	0.018	56.3	0.42
39	0.35	0.56	0.021	50.8	0.47
11	0.31	0.47	0.018	55.0	0.51
38	NA	NA	0.022	47.5	0.37
60	0.43	0.83	0.021	48.7	0.52
37	0.32	0.50	0.023	47.0	0.56
17	0.35	0.56	0.022	47.6	0.51
56	0.38	0.67	0.017	57.6	0.42
31	NA	NA	0.019	56.7	0.51
46	0.37	0.64	0.020	52.6	0.57
24	0.34	0.52	0.021	48.7	0.48
12	0.38	0.62	0.021	48.2	0.50
42	0.35	0.55	0.019	56.2	0.55
14	0.35	0.58	0.017	63.0	0.46
41	NA	NA	0.016	67.2	0.43
5	0.33	0.52	0.016	65.1	0.55

Appendix 5: Continues.

Family	HI	BI	ST	ST*	CS
55	0.33	0.51	0.020	55.8	0.48
52	0.44	0.86	0.019	57.1	0.54
33	0.35	0.56	0.021	50.1	0.60
35	0.34	0.56	0.023	43.9	0.55
58	NA	NA	0.017	61.3	0.59
47	NA	NA	0.022	59.1	0.66
23	0.46	0.94	0.017	62.5	0.57
1	0.43	0.78	0.020	53.0	0.61
16	NA	NA	0.014	78.5	0.63
48	0.42	0.74	0.022	57.1	0.59
15	0.39	0.71	0.017	64.3	0.63
50	0.35	0.54	0.018	45.6	0.65
19	0.35	0.55	0.023	47.2	0.74
40	NA	NA	0.020	49.3	0.47
10	NA	NA	0.018	59.7	0.77
44	NA	NA	0.020	50.6	0.69
54	NA	NA	0.018	56.1	0.75

Appendix 5: Continues

Field Traits	Greenhouse Traits															
	FH2	FH4	FH6	FH8	FH10	FH12	FH14	FH16	FH18	TH20	TH22	TH24	TH26	TH28	TH30	TH32	TH34
h_i^2	0.745	0.729	0.766	0.730	0.722	0.729	0.767	0.775	0.777	0.699	0.686	0.678	0.650	0.636	0.596	0.540	0.518
	0.121	**0.120**	**0.123**	**0.120**	**0.119**	**0.120**	**0.124**	**0.124**	**0.125**	**0.117**	**0.115**	**0.114**	**0.112**	**0.111**	**0.105**	**0.098**	**0.095**
h_f^2	0.906	0.903	0.908	0.902	0.901	0.902	0.908	0.909	0.909	0.866	0.864	0.862	0.856	0.852	0.841	0.824	0.816
	0.250	**0.247**	**0.253**	**0.246**	**0.245**	**0.246**	**0.253**	**0.254**	**0.254**	**0.216**	**0.214**	**0.213**	**0.209**	**0.206**	**0.198**	**0.187**	**0.183**
h_i^2	0.681	0.674	0.726	0.707	0.702	0.680	0.682	0.685	0.688	0.622	0.558	0.554	0.487	0.441	0.401	0.371	0.362
	0.114	**0.113**	**0.119**	**0.117**	**0.117**	**0.114**	**0.114**	**0.115**	**0.115**	**0.108**	**0.104**	**0.100**	**0.091**	**0.085**	**0.079**	**0.075**	**0.073**
h_f^2	0.896	0.894	0.901	0.900	0.899	0.895	0.895	0.896	0.896	0.847	0.838	0.828	0.805	0.785	0.766	0.750	0.744
	0.239	**0.237**	**0.247**	**0.243**	**0.242**	**0.237**	**0.238**	**0.238**	**0.239**	**0.203**	**0.197**	**0.190**	**0.176**	**0.166**	**0.157**	**0.150**	**0.148**

Appendix 6: Heritability estimates for the greenhouse traits when families with extreme rank changes were removed for correlation analysis with site A (upper part of the table) and site B (lower part of the table). Values in bold font are standard errors.

Field Traits	Greenhouse Traits															
	TH36	SH2	SH4	SH6	SH8	SH10	SH12	SH14	SH18	SH18	k	k^+	r	r^+	$t_{0.5}$	$t_{0.5}^+$
h_l^2	0.515	0.273	0.233	0.338	0.395	0.404	0.377	0.329	0.318	0.314	0.795	0.210	0.214	0.144	0.471	0.222
	0.094	**0.063**	**0.058**	**0.072**	**0.080**	**0.081**	**0.078**	**0.071**	**0.069**	**0.069**	**0.126**	**0.056**	**0.048**	**0.049**	**0.087**	**0.058**
h_f^2	0.814	0.635	0.594	0.689	0.722	0.730	0.714	0.681	0.673	0.670	0.912	0.552	0.688	0.452	0.843	0.567
	0.182	**0.123**	**0.113**	**0.137**	**0.150**	**0.151**	**0.146**	**0.135**	**0.133**	**0.132**	**0.258**	**0.108**	**0.115**	**0.092**	**0.189**	**0.110**
h_l^2	0.357	0.192	0.163	0.178	0.193	0.196	0.197	0.193	0.200	0.192	0.687	0.115	0.251	0.036	0.378	0.195
	0.073	**0.053**	**0.049**	**0.051**	**0.053**	**0.053**	**0.053**	**0.053**	**0.054**	**0.052**	**0.115**	**0.047**	**0.054**	**0.042**	**0.074**	**0.055**
h_f^2	0.740	0.541	0.498	0.522	0.543	0.546	0.547	0.543	0.552	0.540	0.896	0.391	0.725	0.163	0.799	0.529
	0.147	**0.103**	**0.096**	**0.100**	**0.104**	**0.104**	**0.105**	**0.104**	**0.105**	**0.103**	**0.239**	**0.085**	**0.127**	**0.064**	**0.160**	**0.104**

Appendix 6: Continues

Field Traits	Greenhouse Traits															
	D24	D30	D36	D54	BL	NL	NSU	MSUL	TB2	BU2	DB	FS	DS	TFS	TDS	DR
h_i^2	0.546	0.473	0.404	0.227	0.550	0.614	0.181	0.465	0.309	0.327	0.225	0.045	0.051	0.151	0.167	0.228
	0.098	**0.088**	**0.078**	**0.060**	**0.098**	**0.106**	**0.077**	**0.102**	**0.063**	**0.066**	**0.082**	**0.074**	**0.075**	**0.077**	**0.078**	**0.082**
h_f^2	0.850	0.826	0.797	0.560	0.945	0.872	0.379	0.635	0.753	0.765	0.428	0.123	0.138	0.328	0.352	0.431
	0.199	**0.182**	**0.165**	**0.111**	**0.305**	**0.217**	**0.105**	**0.148**	**0.142**	**0.147**	**0.112**	**0.081**	**0.082**	**0.100**	**0.103**	**0.113**
h_i^2	0.410	0.340	0.296	0.169	0.476	0.510	0.170	0.480	0.539	0.541	105	0.027	0.036	0.071	0.082	0.129
	0.079	**0.068**	**0.062**	**0.054**	**0.087**	**0.093**	**0.076**	**0.103**	**0.097**	**0.097**	**0.078**	**0.077**	**0.077**	**0.077**	**0.077**	**0.078**
h_f^2	0.802	0.765	0.735	0.478	0.935	0.846	0.364	0.645	0.854	0.855	0.245	0.076	0.099	0.179	0.201	0.287
	0.167	**0.149**	**0.137**	**0.098**	**0.275**	**0.194**	**0.103**	**0.150**	**0.200**	**0.202**	**0.092**	**0.078**	**0.080**	**0.086**	**0.088**	**0.097**

Appendix 6: Continues

Appendix 7: Multiple comparison of family means for field sites A and B, and greenhouse height. Means with the same letter are not significantly different.

FIELD SITE A

Duncan Grouping	Mean	N	FAM
A	123.706	34	1
A			
B A	122.061	33	2
B A			
B A	121.900	30	26
B A			
B A	121.240	25	5
B A			
B A C	118.778	27	53
B A C			
B D A C	116.821	28	18
B D A C			
E B D A C	114.967	30	39
E B D A C			
E B D A C F	112.871	31	52
E B D A C F			
E B D A G C F	112.208	24	50
E B D A G C F			
E B D H A G C F	110.800	30	36
E B D H A G C F			
E B I D H A G C F	110.000	25	4
E B I D H A G C F			
E B I D H A G C F	109.423	26	51
E B I D H A G C F			
E J B I D H A G C F	107.906	32	10
E J B I D H A G C F			
E J B I D H A G C F	106.913	23	32
E J B I D H A G C F			
K E J B I D H A G C F	106.138	29	25
K E J B I D H G C F			
K E J B I D H L G C F	104.290	31	15
K E J B I D H L G C F			
K E J B I D H L G C F	104.273	33	37
K E J I D H L G C F			
K E J I D H L G C F	103.000	24	42
K E J I D H L G C F			
K E J I D H L G C F	102.647	34	55
K E J I D H L G C F			
K E J M I D H L G C F	101.214	28	22
K E J M I D H L G C F			
K E J M I D H L G C FN	100.897	29	56
K E J M I D H L G FN			
K E J M I D H L G FN	100.345	29	34
K E J M I D H L G FN			
K E J M I D H L G O FN	98.600	25	49
K E J M I D H L G O FN			
K E J M I D H L G O FN	98.500	30	23
K E J M I H L G O FN			
K E J M I P H L G O FN	97.852	27	35
K E J M I P H L G O FN			

| | | |

Q	S	R			
Q	S	R	72.233	30	46
	S	R			
	S	R	71.071	28	3
	S				
	S		64.083	24	57

FIELD SITE B

Duncan Grouping	Mean	N	FAM
A	190.12	33	51
A			
B A	182.24	33	17
B A			
B A C	178.00	35	3
B A C			
B D A C	175.79	34	31
B D A C			
B D A C	175.75	36	10
B D A C			
E B D A C	174.65	31	52
E B D A C			
E B D A C	174.16	32	4
E B D A C			
E B D A C	173.30	33	5
E B D A C			
E B D A C F	172.70	33	55
E B D A C F			
E B D A C F	171.91	34	32
E B D A C F			
E B D A C F	170.43	35	16
E B D A C F			
E B D A G C F	169.27	33	18
E B D A G C F			
E B D A G C F	169.27	30	22
E B D A G C F			
E B D A G C F	167.17	36	45
E B D A G C F			
E B D A G C F	166.97	36	13
E B D A G C F			
E B D A G C F	165.30	33	1
E B D A G C F			
E B D A G C F	164.40	35	39
E B D G C F			
E B D H G C F	162.83	36	36
E B D H G C F			
E B D H G C F	162.06	33	50
E B D H G C F			
E B D H G C F	162.00	27	43
E B D H G C F			
E B D H G C F	160.94	32	53
E B D H G C F			
E B D H G C F	160.88	34	11
E B D H G C F			
E B D H G C F	160.85	33	27
E B D H G C F			
E B D H G C F	158.66	32	7
E B D H G C F			
E B D H G C F	158.33	33	14
E B D H G C F			
E B D I H G C F	157.25	28	21
E B D I H G C F			
E B D I H G C F	157.23	35	23

E	B	D	I	H	G	C	F					
E	B	D	I	H	G	C	F		157.14		35	38
E	B	D	I	H	G	C	F					
E	B	D	I	H	G	C	F		156.94		34	56
E	B	D	I	H	G	C	F					
E	B	D	I	H	G	C	F		155.70		33	26
E	B	D	I	H	G	C	F					
E	B	D	I	H	G	C	F		154.97		34	44
E	B	D	I	H	G	C	F					
E	B	D	I	H	G	C	F		154.88		32	35
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		154.48		33	34
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		154.07		27	58
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		153.69		32	25
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		153.19		36	48
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		152.94		36	41
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		152.89		35	15
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		152.74		34	12
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		152.35		31	28
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		152.10		29	33
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		151.89		35	2
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		151.06		35	49
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		151.00		36	37
E		D	I	H	G	C	F					
E		D	I	H	G	C	F		149.90		29	46
E		D	I	H	G		F					
E		D	I	H	G		F		149.53		34	9
E		D	I	H	G		F					
E		D	I	H	G		F		149.39		33	42
E		D	I	H	G		F					
E		D	I	H	G		F		148.12		34	8
E			I	H	G		F					
E			I	H	G		F		147.09		35	47
			I	H	G		F					
			I	H	G		F		145.12		33	59
			I	H	G							
			I	H	G				142.18		33	60
			I	H	G							
			I	H	G				142.06		31	24
			I	H	G							
			I	H	G				141.64		33	40
			I	H	G							
			I	H	G				141.30		30	54
			I	H								
	J		I	H					135.03		33	20
	J		I									

J	I	129.85	34	19
J				
J		115.94	36	57

GREENHOUSE 36-WEEK HEIGHT (TH36)

Duncan Grouping	Mean	N	FAM
A	321.30	23	2
B	251.88	25	20
B			
C B	246.00	20	3
C B			
C B D	241.44	16	6
C B D			
C B D	239.33	21	8
C B D			
C E B D	238.95	19	28
C E B D			
F C E B D	235.35	26	7
F C E B D			
F C E B D	233.23	13	21
F C E B D			
F C E B D G	229.15	20	27
F C E B D G			
F C E B H D G	224.18	28	13
F C E B H D G			
F C E I B H D G	219.64	22	34
F C E I B H D G			
F C E I B H D G	219.58	26	49
F C E I B H D G			
F C J E I B H D G	218.76	17	18
F C J E I B H D G			
F K C J E I B H D G	216.58	24	22
F K C J E I B H D G			
F K C J E I B H D G	215.08	24	4
F K C J E I B H D G			
F K C J E I B H D G	214.70	20	32
F K C J E I B H D G			
L F K C J E I B H D G	213.08	12	25
L F K C J E I B H D G			
L F K C J E I B H D GM	211.50	24	9
L F K C J E I B H D GM			
L F K C J E I B H D GM	208.85	26	45
L F K C J E I B H D GM			
L F K C J E I B H D GM	208.58	24	26
L F K C J E I B H D GM			
L F K C J E I B H D GM	208.50	24	51
L F K C J E I B H D GM			
L F K C J E I B H D GM	208.06	16	43
L F K C J E I B H D GM			
L F K C J E I B H D GM	207.52	23	59
L F K C J E I B H D GM			
L F K C J E I B H D GM	207.04	24	39
L F K C J E I B H D GM			
L F K C J E I B H D GM	206.32	28	57
L F K C J E I B H D GM			
L F K C J E I B H D GM	205.93	14	36
L F K C J E I B H D GM			
L F K C J E I B H D GM	205.22	9	38

L	F	K	C	J	E	I	B	H	D	GM			
L	F	K	C	J	E	I	B	H	DNGM		203.89	27	53
L	F	K	C	J	E	I	B	H	DNGM				
L	F	K	C	J	E	I	B	H	DNGM		203.21	24	31
L	F	K	C	J	E	I	B	H	DNGM				
L	F	K	C	J	E	I	B	H	DNGM		201.06	17	56
L	F	K	C	J	E	I		H	DNGM				
L	F	K	C	J	E	I	O	H	DNGM		200.06	18	11
L	F	K	C	J	E	I	O	H	DNGM				
L	F	K	C	J	E	I	O	H	DNGM		199.54	24	17
L	F	K	C	J	E	I	O	H	DNGM				
L	F	K	C	J	E	I	O	H	DNGM		196.83	23	60
L	F	K	C	J	E	I	O	H	DNGM				
L	F	K	C	J	E	I	O	H	DNGM		194.68	25	12
L	F	K		J	E	I	O	H	DNGM				
L	F	K	P	J	E	I	O	H	DNGM		194.25	20	55
L	F	K	P	J	E	I	O	H	DNGM				
L	F	K	P	J	E	I	O	H	DNGM		194.00	27	24
L	F	K	P	J	E	I	O	H	DNGM				
L	F	K	P	J	E	I	O	H	DNGM		193.50	24	14
L	F	K	P	J	E	I	O	H	DNGM				
L	F	K	P	J	E	I	O	H	DNGM		192.25	28	37
L	F	K	P	J	E	I	O	H	DNGM				
L	F	K	P	J	E	I	O	H	DNGM		192.10	29	42
L	F	K	P	J	E	I	O	H		NGM			
L	F	K	P	J	E	I	O	H	QNGM		187.39	23	46
L	F	K	P	J		I	O	H	QNGM				
L	F	K	P	J		I	O	H	QNGM		186.62	26	5
L		K	P	J		I	O	H	QNGM				
L		K	P	J	R	I	O	H	QNGM		180.84	25	52
L		K	P	J	R	I	O	H	QNGM				
L		K	P	J	R	I	O	H	QNGM		177.68	25	33
L		K	P	J	R	I	O	H	QN	M			
L	S	K	P	J	R	I	O	H	QN	M	172.79	14	41
L	S	K	P	J	R	I	O		QN	M			
L	S	K	P	J	R	I	O		QN	M	171.06	16	58
L	S	K	P	J	R	I	O		QN	M			
L	S	K	P	J	R	I	O		QN	M	170.15	20	35
L	S	K	P	J	R	I	O		QN	M			
L	S	K	P	J	R	I	O		QN	M	167.73	22	47
L	S	K	P	J	R		O		QN	M			
L	S	K	P	J	R		O		QN	M	167.41	17	16
L	S	K	P		R		O		QN	M			
L	S	K	P		R		O		QN	M	166.33	21	1
L	S		P		R		O		QN	M			
L	S		P		R		O		QN	M	162.08	24	23
L	S		P		R		O		QN	M			
L	S		P		R		O		QN	M	161.57	21	48
	S		P		R		O		QN	M			
	S		P		R		O		QN	M	160.63	19	15
	S		P		R		O		QN				
	S		P		R		O		QN		153.04	24	50
	S		P		R		O		Q				
	S		P		R		O		Q		149.45	20	40
	S		P		R				Q				
	S		P		R				Q		144.13	24	19
	S				R				Q				

S	R	Q	138.41	17	44
S	R				
S	R		133.83	18	10
S					
S			124.00	22	54